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CONTENTS

An Experimental Test of the Predator Satiation Hypothesis: At What Level Might It Apply? .... Stephanie S. Romañach and Douglas J. Levey 1
Analysis of Commercial Selenium-Supplement Tablets .... Kathleen M. Carvalho, Robert F. Benson, Francis A. Booth, M. Jordan Collier, and Dean F. Martin 8
Florida's Wax Palm: The Silver Form of *Serenoa repens* (Arecaceae) .... Frederick B. Essig, Y. Renea Taylor, and Diane TeStrake 13
Wildlife Use of a Created Wetland in Central Florida .... Donald M. Kent and Michael A. Langston 17
Influence of Distance and Post-Fire Recovery on Accuracy of Hand-Held Radiotelemetry in Forested Landscapes in Southwest Florida .... Martin B. Main, Ellen Cheng, Betty Harper, and Larry W. Richardson 20
Inventory of Fishes of Everglades National Park .... William F. Loftus 27
The Influence of Seawalls and Revetments on the Presence of Seagrass in the Indian River Lagoon, A Preliminary Study .... Steve Nielsen, Bill Eggers, and Sharon Collins 48
Book Review .... Frederick B. Essig 62
Books Received 63

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QUARTERLY JOURNAL OF THE FLORIDA ACADEMY OF SCIENCES

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Biological Sciences

AN EXPERIMENTAL TEST OF THE PREDATOR SATIATION HYPOTHESIS: AT WHAT LEVEL MIGHT IT APPLY?

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ABSTRACT: *The Predator Satiation Hypothesis posits that synchronous masting of fruits or nuts will maximize the probability of satiating local seed predators, allowing some seeds to escape predation and germinate. Although the hypothesis is usually applied at the population level to explain synchronous reproduction of many individuals, it also might apply at the individual level. In fact, if individual trees were able to satiate local predators, it would reduce selection for synchronous reproduction at the population level. We tested whether individual laurel oaks,* Quercus hemisphaerica, *could satiate their acorn predators. We simulated mast conditions by adding many acorns under the canopies of some trees, while adding few to other, non-mast trees. We then monitored the rate of acorn removal from both mast and non-mast trees. We predicted that non-mast trees would have a higher rate of acorn removal because they would not be able to satiate the major seed predator at our study site, the gray squirrel,* Sciurus carolinensis. *The results did not support our prediction; we found no difference in the removal rate of acorns from mast and non-mast trees. This may be attributable to two characteristics of our study site: the unusually high density of gray squirrels during the year of our study, and the size of* Q. hemisphaerica *trees at the site, which may have been too small to produce enough acorns to satiate such a large number of seed predators. We conclude that the Predator Satiation Hypothesis is most likely to find support at the level of a population, not at the level of individual trees. Predator satiation appears to be a population level phenomenon, with benefits to individual trees.*

ACORNS are a key food source for many animals (Martin et al., 1951; Van Dersal, 1940; Sork et al., 1983; Smith and Scarlett, 1987). Their importance is demonstrated by the management efforts given to acorn crops.

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One such management technique is to eliminate factors that delay germination, thereby ensuring that a seedling will establish before a seed predator consumes the acorn. However, all management techniques are complicated by large variation in acorn crop sizes from one year to the next—a pattern called masting.

Masting occurs in cycles that are species specific (Koenig and Knops, 1995). One reason is that different oak species require different numbers of years for their acorns to mature. This is an important factor in determining the number of years between large and small crops (Koenig and Knops, 1995). During a mast year, all oaks in a population of a particular species produce enormous crops in synchrony. Such populations can consist of individuals as far apart as 2,500 km (Koenig and Knops, 1997). Masting cycles not only have dramatic effects on populations of acorn consumers (Ostfeld et al., 1996; McShea and Schwede, 1993), but also on economically and ecologically important organisms such as gypsy moths, *Lymantria dispar,* and deer mice, *Peromyscus leucopus,* which harbor the tick vector for the bacteria (*Borrelia burgdorferi)* that causes Lyme disease in humans (Jones et al., 1998). When mice are abundant, they suppress outbreaks of gypsy moths. However, abundant mice also increase the risk of Lyme disease (Jones et al., 1998). Understanding such mast-dependent ecological chain reactions is important for predicting and managing forests and for human health. Yet, we do not even understand the evolutionary basis for why some tree species mast in the first place (e.g., Koenig et al., 1994).

Four main hypotheses explain why masting occurs. First, the Resource Matching Hypothesis states that seed crops are determined by resource levels that fluctuate annually, giving rise to the masting patterns observed (Norton and Kelly, 1988). Second, the Seed Dispersal Hypothesis posits that masting patterns are due to competition among trees for a limited number of animals that disperse their seeds (Ims, 1990). Third, the Wind Pollination Hypothesis proposes that wind pollinated trees produce flowers and fruit in synchrony to assure adequate concentration of pollen during a mast year (Nilsson and Wästljung, 1987; Norton and Kelly, 1988). Finally, the Predator Satiation Hypothesis predicts that during mast years, oaks will produce more seeds than can be eaten by local seed predators, so that some escape predation and germinate (Silvertown, 1980). Implied in the Predator Satiation Hypothesis is that seed predators will starve or move elsewhere during non-mast years, when few or no seeds are produced.

This study addresses the Predator Satiation Hypothesis. At issue is the scale at which predator satiation occurs. In particular, to what extent can a single tree satiate its local seed predators? During a non-mast year, we simulated mast conditions for some trees and monitored acorn removal by seed predators beneath these and control (non-mast) trees. If the Predator Satiation Hypothesis holds on the level of an individual, more acorns should be removed from non-mast trees because their predators would not be satiated. This result would demonstrate a selective advantage to masting for individ-

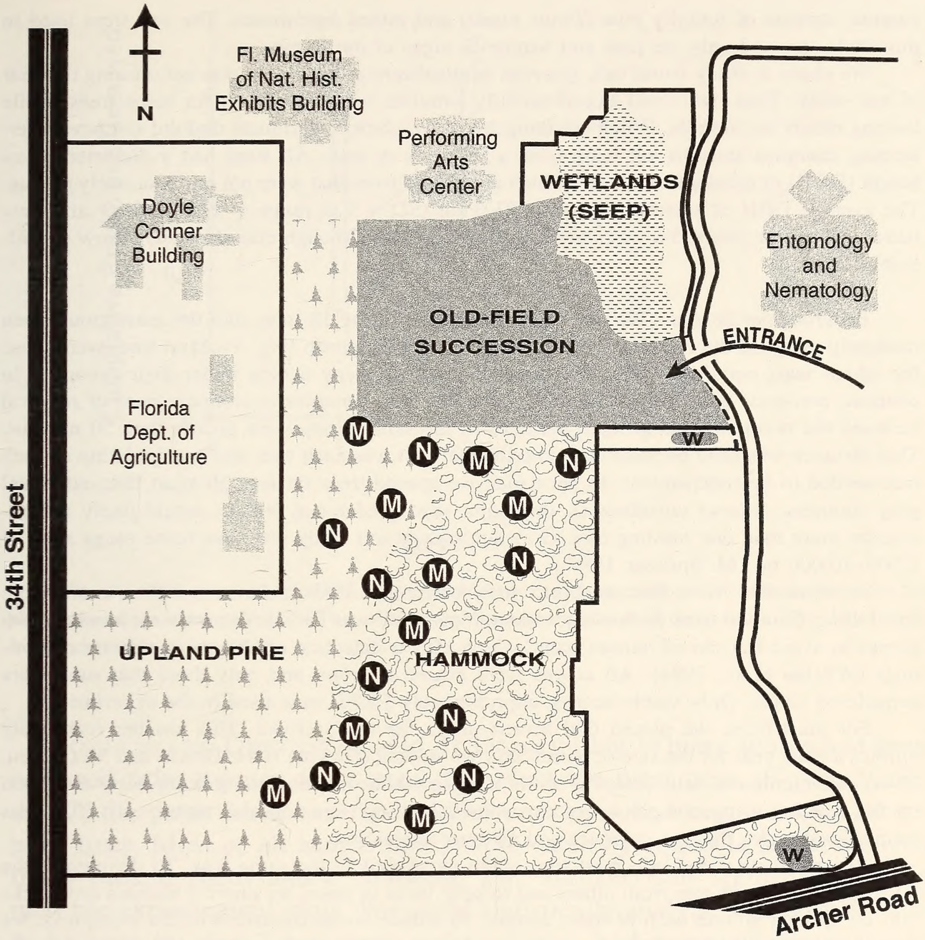

FIG. 1. Map of the Natural Area Teaching Laboratory showing the distribution of mast (M) and non-mast (N) trees within the upland pine and hammock habitats. (Figure adapted from http://csssrvr.entnem.ufl.edu/~walker/natl.htm.) "W" denotes wetlands.

ual trees and would call into question the Predator Satiation Hypothesis for synchronous masting at the population level. If, on the other hand, non-mast trees do not have a larger proportion of acorns removed, this would suggest a selective advantage of synchronous masting at the population level.

METHODS—*Study site and species*—This experiment was conducted at the Natural Area Teaching Laboratory (NATL) at the University of Florida, Gainesville, Florida. NATL is a 40-acre forest composed of three approximately equal sized habitats: upland pine, hammock, and old-field succession (Figure 1). The upland pine habitat is a well-drained, predominantly sandy-soiled, longleaf pine *(Pinus palustris)* area and is burned every 3 to 5 years. The hardwood hammock is a mesic habitat composed of trees such as oaks and hickories (e.g., *Quercus* spp., *Carya glabra),* along with understory shrubs *(*e.g., *Vaccinium arboreum*). The old-field succession consists of loblolly pine (*Pinus taeda*) and mixed hardwoods. The oak trees used in this study spanned only the pine and hammock areas of the forest.

We chose to study laurel oak, *Quercus hemisphaerica,* because it was not masting the year of our study. Thus, we could experimentally simulate mast conditions for some trees, while leaving others as controls. When selecting trees, we chose individuals that did not have overlapping canopies and did not hang over a firebreak or trail. All trees had a diameter breast height (DBH) of greater than 14 cm, which eliminated trees that were not reproductively mature. The average DBH of selected trees was 23.6 cm (SD = 8.0, range = 14.6 to 36.0 cm). Few laurel oaks at the study site were larger than those used, although elsewhere they grow considerably larger.

Experimental design—We randomly assigned 9 of the 18 trees into the mast group, then randomly assigned the remaining 9 trees to the non-mast group (Fig. 1). Mast trees were those for which mast conditions were simulated by placing many acorns under their canopies. In contrast, non-mast trees had few acorns put under their canopies to compare rates of removal between the two treatment groups. All trees of the same group were greater than 50 m apart. This distance was used because our experimental unit was each tree, and manipulation of each tree needed to be independent. In particular, we spaced trees far enough apart that individual gray squirrels, *Sciurus carolinensis,* the major seed predator at NATL, would likely not encounter more than one masting tree. Gray squirrels at our study site have home range sizes of 2,500–10,000 m^2 (M. Spritzer, 1997).

At other sites, we collected acorns from November 1997 to January 1998. Acorns were still falling from the trees in January, although peak fall was earlier. Acorns were handled with gloves to avoid transfer of human scent, which affects detection of objects by terrestrial mammals (Whelan et al., 1994). All acorns were placed in water and only those that sunk were considered viable. Only viable acorns, approximately 5,850, were used in the experiment.

For mast trees, we placed 600 acorns under the tree's crown. This number reasonably mimics a mast year for the size of laurel oaks we studied (Downs, 1944; Downs and McQuillen, 1944). We monitored daily removal of 50 of these 600 acorns beginning in the early afternoon on the day following completion of experimental set-up. For non-mast trees, only 50 acorns were placed under the tree canopies and all were monitored.

Acorns of mast and non-mast trees were monitored in the same way. To distinguish the 50 acorns under each tree from others and to keep them in place, we drove 3 wooden toothpicks into the ground around each of these acorns. To reduce conspicuousness of the toothpicks, we dyed them dark brown, which generally matched the color of the sticks and leaf litter on the ground. The toothpicks did not protrude above the top of the acorns; they did not appear conspicuous. To easily relocate the acorns, we placed them approximately 31 cm away from the tree trunks in a circular pattern. So that attention would not be drawn to a potential food source whenever a toothpick was spotted, we scattered other dyed toothpicks under the canopy of all trees used in the study.

Trees were paired for data analysis; each mast tree was paired with a non-mast tree, giving a total of nine pairs. Trees were first grouped according to habitat to control for heterogeneity of the forest (i.e. oaks in hammock area were not grouped with oaks in the pine area). After this grouping, trees with similar DBH were paired to control for differences in crop sizes. Acorns were placed under both trees of each pair on the same day.

The experiment was set up on 19 and 20 January, 1998. We monitored acorn removal from 21 to 23 January, 1998. The experiment was terminated on 23 January because all marked acorns had been removed from all trees.

Statistical methods—Data were analyzed non-parametrically with a Wilcoxon matched-pairs signed-rank test because the data (i.e., trees) were paired. Also, the acorns were removed rapidly and completely, yielding a small sample of days and resulting in non-normal distributions of percentages of acorns removed across populations of mast and non-mast trees. Thus, the statistical test we had planned to use, a repeated measures ANOVA, was inappropriate.

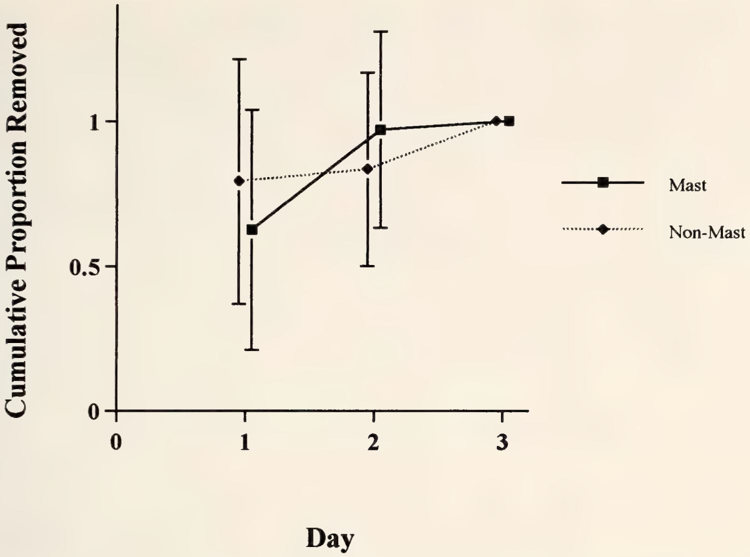

FIG. 2. Cumulative proportions of acorns removed from mast and non-mast trees for the three days data were collected. The vertical bars represent standard deviations. The data points have been off-set for clarity.

RESULTS AND DISCUSSION—On 21 January (day 1) more acorns had been removed from the non-mast trees than from the mast trees (Figure 2). By day 2, the pattern had reversed and more acorns had been removed from mast trees. Most or all acorns likely were eaten by squirrels, as we noticed many broken shells and a colleague (M. Spritzer) saw squirrels foraging near our experimental plots. We could statistically analyze data only for day 1, because by day 2 too many pairs of trees had complete removal and therefore could not be included in the analysis. We found no significant difference in the number of marked acorns removed from mast and non-mast trees ($T = 9$, $N = 7$, $p > 0.05$; test based on seven pairs because two pairs had differences of zero and therefore had to be excluded).

We found no effect of masting on acorn removal at the level of individual trees. Equal removal from mast and non-mast trees on the first day of monitoring, plus complete removal of all acorns by day 3 clearly indicates that single laurel oaks of the size we studied cannot satiate local predator populations when squirrel density is high. Consequently, selection is likely to favor masting at the population level, assuming satiation is feasible at that scale.

A key factor determining whether acorn predators can be satiated was not addressed in our study. In particular, predator satiation depends not only on acorn abundance, but also predator abundance. Generally, in the year following a mast year, acorn predators experience an increase in their population sizes (McShea and Schwede, 1993; Wolff, 1996). Indeed, at our study site laurel oak masted the year prior to our study and, as a result, the gray squirrel population density was unusually high. Trapping data show the density to be 14 squirrels/ha in 1997 (M. Spritzer, 1997). In this context, it is not surprising that all acorns were quickly consumed.

Rapid and complete removal of 6,000 acorns in 3 days is noteworthy because one of the primary predictions of the Predator Satiation Hypothesis is that synchronous masting should occur in an area that experiences heavy seed predation (Silvertown, 1980). During the next couple of years, laurel oak at our study site should produce few or no acorns and the squirrel population should begin to decline as a result (Kurzejeski, 1989). If acorn predation is low by the next laurel oak mast year (i.e., low seed predator population sizes), some seeds may survive to germinate, thereby providing an advantage to individuals that irregularly mast in synchrony.

Finally, our results raise the question of why relatively small trees mast at all. Even if all oaks at our site had each produced 600 acorns, it is likely that predation on those acorns would have been complete. If, however, our site had been dominated by huge laurel oaks, each producing 10,000 acorns, some acorns would likely have escaped consumption. We suggest that the reason small individuals mast is because the size of an individual oak's neighbors is essentially impossible to predict. By producing even small mast crops, small oaks can take advantage of predator satiation by nearby and much larger individuals, as well as taking advantage of years in which acorn predator populations are low. Indeed, the key to understanding predator satiation in oaks that mast seems to lie in the unpredictability of masting cycles, the crop size of neighboring trees, and the population density of predators.

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ANALYSIS OF COMMERCIAL SELENIUM-SUPPLEMENT TABLETS

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Abstract: *Commercially available selenium-supplement tablets, obtained from a supermarket and a health food store in several lots were analyzed to compare reported and observed values of total selenium. Atomic absorption spectrometry with a hydride generator was used, and the results were confirmed for selected lots using inductively coupled plasma (ICP) spectrometry. Results indicate more variation than might be suspected. Several lots contained a significantly higher amount of selenium than reported with one lot having 50% more. One brand contained only 20–25% of the reported concentration, a significantly lower amount. Tablets were analyzed and compared to determine which brand, if any, had the most reliable amount per tablet.*

Selenium has had a checkered history. It is now regarded as an essential element (Schroeder et al., 1970), as well as an anticarcinogenic agent (Rosenfeld and Beath, 1964). There was a time, however, when it was most notable for effects of excess selenium, as concentrated in seleniferous plants, e.g., loco weed. These plants were consumed by cattle starved for forage during the Great Depression and as a consequence of the toxic level of selenium consumed, toxic effects, colloquially termed "Devil's Disease" were noted (Shamberger, 1983). In addition, during the 1950s, selenium was thought to be a carcinogen. One reason for this was the observation of liver tumors in rats owing to induction of cirrhosis after the rats had been fed selenium (Nelson et al., 1943). After this observation, more investigations of selenium and its relationship with cancer were explored. Six studies exploring the issue of selenium's carcinogenicity were reviewed with the following conclusions (Hegsted, 1970). Three of six studies that identified selenium as a carcinogen were found to be flawed, with inadequate experimental designs and unnaturally high levels of selenium. Three studies, which identified selenium as anticarcinogenic, were found to be properly planned and controlled. The FDA therefore concluded, "judicious administration of selenium derivatives to domestic animals would not constitute a carcinogenic risk" (U. S. FDA, 1973).

Now, however, selenium is recognized as an essential element. The absence of adequate selenium from the human diet leads to a congestive heart disease known as Keshan disease, a condition associated with muscle development in hearts (Shamberger, 1983).

In addition, it was suggested more than 80 years ago that selenium compounds be used in cancer chemotherapy (Combs, 1986). The average intake of selenium in the United States has been reported to be as low as 25 μg/2400 kcal. Since selenium is a trace element, a majority of the selenium in our diets is from the foods we intake. In 1996, it was determined that in humans, 40% of the selenium intake is from meat, 24% from dairy products and eggs, and 11% from seafood and 19% from cereal products (Frankenberger and Engberg, 1998). Therefore, since most foods are not enriched with selenium, the best alternative is a selenium supplement tablet. The recommended dosage of selenium supplements is 50–200 μg per day (NRC, 1983). For a diet supplement that contains 100 μg per tablet, it is an easily calculated dosage.

Since commercially sold selenium supplements tablets are not federally regulated, the amount of selenium actually contained in the tablets seemed worth investigating. The present study arose from the hypothesis that tablets would contain no less than the stated amount of selenium, and they might actually contain more. In this study, commercial supplement tablets were analyzed for actual selenium content. Several different brands were chosen, and different lots from each brand were analyzed.

MATERIALS AND METHODS—*Sources*—Samples were obtained from three stores, recorded as Brands A, B, C, that were obtained respectively from supermarket A, supermarket B, and health food store C.

Instrumentation—A Varian SpectraAA-100 atomic absorption spectrometer, equipped with a selenium lamp (Fischer Scientific), was used for the quantification of selenium in the tablets. A hydride generation apparatus (Fig. 1), constructed by the Department of Chemistry glassblower, was used to analyze the amount of H_2Se gas given off from each tablet.

Solutions—15.8 *M* Nitric acid and 12.1 *M* hydrochloric acid, obtained from Fisher Scientific, were certified ACS reagent grade. Sodium hydroxide was obtained from Fisher Scientific certified ACS grade at >98% purity. Sodium borohydride (>98% purity) and selenium dioxide (>99% purity) were obtained from Acros Organics. A solution of selenium was prepared as a primary standard for further dilution from an accurately weighed amount of SeO_2. A primary standard at 1000 ppm of Se was prepared by adding 1.4054g of selenium dioxide and dissolving in 6%(w/w) HCl to 1 liter. Calibration standards ranging from 1 to 10 ppm were prepared by using the appropriate volume of primary standard and diluting with 6%(w/w) HCl. A fresh solution of $NaBH_4$ was prepared before each analysis by dissolving 3.0 g of $NaBH_4$ and 2.5 g NaOH in distilled water and diluting to 500 mL.

AAS procedure—A calibration curve was established for the selenium samples by analyzing each standard in the following manner. First, 6 mL of $NaBH_4$ was injected through a septum into the hydride generation apparatus. Next, exactly 4 mL of each standard was placed in the hydride generation apparatus with a syringe. A flow rate of 3.2 ml/min was used with nitrogen gas as the purge gas. The amount of H_2Se was measured for each sample and compared with the calibration curve.

Figure 1 Hydride Generation Apparatus

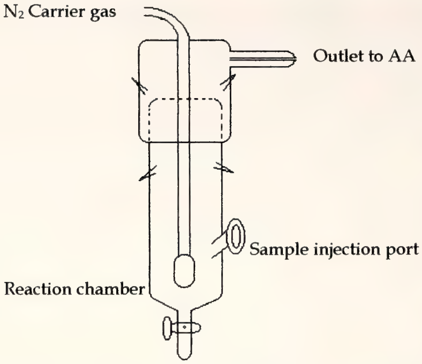

FIG. 1. Schematic representation of hydride generation apparatus.

ICP measurements—ICP measurements were done on a selected number of samples were conducted at two different laboratories for method validity and verification. At Savannah Laboratories, a Thermo Jarrell Ash Trace Analyzer was also used for a selected number of representative samples for purposes of confirmation. The samples were analyzed at ambient temperature 20–21°C and a humidity of 38–40%. For each analysis by ICP, a minimum sample of 1-gram dry weight was needed; therefore four supplement tablets were ground into a powder, weighed and then placed in a 150-mL Teflon beaker. Next, 5-mL of 15.8 *M* nitric acid and 5-mL of deionized water were added. The sample was covered with a watch glass and refluxed for 10–15 minutes without boiling (90–95°C). The sample was then allowed to cool, another 5-mL of 15.8 *M* nitric acid was added and the sample was refluxed for 30 minutes. This step was repeated, then 2-mL of deionized water and 3-mL of 30% hydrogen peroxide were added slowly, and the mixture was heated until effervescence ceased. Finally, 5-mL of 12.1 *M* hydrochloric acid was added and the mixture was refluxed for 10 to 15 min. The sample was cooled to room temperature, then diluted to 100 mL with deionized water. Then a 1-mL aliquot of sample was injected in the ICP, and each sample was analyzed three times. A matrix spike consisting of selenium, lead, calcium, and other elements was used with the controls and also the samples as part of the standard calibration for the instrument. Calibration of the instrument was done every fifth sample.

At Constellation Technology Corporation, a Thermo Jarrell Ash IRIS Advantage ICP-AES was used for samples from Store C, Lot 2. One tablet of mass 300 mg was dissolved in 10 mL of 15.8 *M* nitric acid and heated to 75°C for one hour. The solution was diluted to 100 mL with 10% (v/v) nitric acid. The calibration curve was constructed using standard solutions containing 0.10, 0.50, 1.0, 5.0, 10.0 ppm Se in 10% (v/v) nitric acid. The sample solution was then analyzed using atomic absorption (AA) and inductively coupled plasma-atomic emission spectroscopy (ICP-AES). The atomic absorption was measured using a Perkin Elmer Model 5100 PC Atomic Absorption Spectrophotometer with a background correction at 196.090 nm. The results from this verification analysis are in Table 1.

RESULTS AND DISCUSSION—Results are summarized in Tables 1 and 2 for the three brands and for the total of nine lots. These results indicate several significant features.

First, the agreement between two methods is good within experimental

TABLE 1. Comparison of AA and ICP analyses of Se content in commercial selenium supplement tablets.

Store	Lot #	AA observed conc (μg)	ICP observed conc (μg)	Reported conc (μg)
A	3	20.0 ± 1.2	25.6 ± 3.2*	100.0 ± 0.1
B	1	117.0 ± 16	108 ± 6.2*	100.0 ± 0.1
C	2	60.1 ± 10.0	62.5 ± 2.0*	50.0 ± 0.1
**C	2	60.0 ± 3.0**	60.0 ± 0.6**	50.0 ± 0.1

* Conducted at Savannah Laboratories.
** Conducted at Constellation Technologies.

error as shown in Table 1. A Student's t-test was performed comparing the means observed for the selected lots, and it was determined, at a 95% confidence level, that there was no significant difference between the two methods. Thus, we have confidence in the atomic absorption results, having been confirmed as they were by the two independent ICP methods for representative samples.

Second, a customer may not assume that the tablets contain the stated amount, according to our results. Eight of the nine lots of three brands did not contain the stated amount, at least within experimental error (Table 2). Brand A seemed to have the most deviation from the reported concentration in lots 2 and 3, having a significantly lower observed concentration. For example, lot 3 of Brand A contained only 20% of the stated amount of selenium, a result that was confirmed by two different methods of analysis. Brands B and C in contrast were consistent with all lots analyzed having a higher concentration than that reported.

Third, the consequences of incorrectly stated amounts may or may not be serious. The lots analyzed that contained a significantly lower amount of selenium than reported is harmful if one is trying to supplement with a recommended daily dosage of selenium and receiving quite less. This can be frustrating, because a consumer is not receiving the amount promised

TABLE 2. Summary of analyses of selenium of commercial selenium supplement tablets by atomic absorption spectrometry.

Store	Lot #	N	Observed conc. (μg)	Reported conc. (μg)
A	1	5 (3 times)	77.4 ± 13.6	100.0 ± 0.2*
A	2	5 (3 times)	35.1 ± 2.4	99.7 ± 0.1*
A	3	5 (3 times)	20.0 ± 1.2	100.0 ± 0.1*
B	1	10 (3 times)	117 ± 16	100.0 ± 0.1*
B	2	5 (3 times)	75.5 ± 8.9	70.0 ± 0.1
B	3	5 (3 times)	86.2 ± 5.5	70.1 ± 0.1*
B	4	5 (3 times)	103 ± 6	70.0 ± 0.3*
C	1	9 (3 times)	95.7 ± 9.8	70.1 ± 0.1*
C	2	5 (3 times)	60.1 ± 10.0	50.0 ± 0.1*

* T-test showed a significant difference at 95% Confidence.

and may not be taking enough to overcome a selenium deficiency. Not having enough selenium in the sample, could lead to serious consequences for a person deficient in selenium or a person taking the recommended dose of 200 μg per day: this person would take two tablets and need ten for the recommended dosage.

On the other hand, consumers who purchase the lots that contained significantly higher amounts of selenium are receiving more for their dollar. However, this can have a bad side also, because if one intakes too much selenium, selenium poisoning can occur. For Brands B and C, the extra selenium is not likely to cause a problem, given the optimum range for selenium in humans. The lots observed with higher amounts of selenium than reported, although these amounts are significantly higher, do not seem to pose a threat if one does not take more than the recommended dosage. This is attributed to the wide safe concentration range of selenium. In conclusion, there was no one brand that did not have significant variation in the amount of selenium and thoughts might be entertained as to whether or not supplements of this kind should be regulated.

Certain aspects of our lives haven't changed over the years: the Latin motto "caveat emptor" still applies, though we tend to assume that samples of substances, vinegar, bleach, hydrogen peroxide, and selenium supplements, contain the advertised amounts. Experience would suggest that is not a valid assumption.

ACKNOWLEDGMENTS—We thank Harry W. Santiago and S. Bradley for their help with the ICP analysis at Savannah Laboratories and William Swartz, John Hayduke and J. Sheffer for the ICP-AES and AA analysis at Constellation Technology, 7887 Bryan Dairy Road, Suite 100, Largo, Florida 33777-1498. We would also like to express our thanks to Mike Arias, Chemistry Department glassblower, for construction of the hydride generation apparatus. Barbara B. Martin served as consulting editor.

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FLORIDA'S WAX PALM: THE SILVER FORM OF *SERENOA REPENS* (ARECACEAE)

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ABSTRACT: Serenoa repens *(Arecaceae) can be found in two distinct color forms: green and "silver." The green form is common throughout the state in pine flatwoods and other upland communities, while the silver form is confined to narrow belts along Florida's Atlantic coast and central ridge. To determine the basis for this color difference we examined the epicuticular wax pattern on the leaf surface, using scanning electron microscopy. We found that in the green form the epicuticular wax formed thin, flat, peeling sheets, while in the silver form the wax formed in thick, irregular patches of fused rod-like extrusions. This striking difference in epicuticular wax accounts for the color difference, but the ecological significance of this feature remains unknown.*

THE saw palmetto, *Serenoa repens* (Bartr.) is an abundant and conspicuous component of the natural vegetation of Florida. This member of the palm family often forms the dominant understory vegetation in pine flatwoods throughout the state, and occurs also in sandhill, scrub, dry prairie, and other upland plant associations. The long roots of this species contain air canals and can penetrate to a meter or more below the water table in low-lying areas. However, the plants grow only where their stems can remain above the high water mark. The boundary between wetland and upland habitats is often sharply defined by the lower limit of saw palmetto growth. Saw palmetto is tolerant of moderate fires and sprouts new leaves within weeks of a burn. The nearly impenetrable thickets created by these clonal palms serve as habitat for numerous animals (Myers and Ewel, 1990), and provided the native Americans with numerous products used for food, medicine and fiber (Duke, 1985).

The silver form of this species, *Serenoa repens* forma *glauca,* according to Moldenke (1967), has long been of interest to horticulturalists and landscapers for the distinctive coloration. The silver form occurs naturally primarily in a narrow, discontinuous belt along Florida's Atlantic coast, stretching from St. Johns County to Dade County, and occasionally inland, particularly along the central ridge in Highlands and Polk counties. Silver *Serenoa* forms dense stands, often adjacent to stands of the green form. The palms are clonal, with procumbent trunks branching and bearing roots, but the extent to which stands represent individual clones is not known. Intermediate forms, determined on the basis of the overall color cast of the leaves, have also been found scattered throughout the state.

The purpose of the present study, conducted as part of the masters thesis of the second author (Taylor, 1995), was to examine the leaves of the different forms of *Serenoa repens* using electron and light microscopies, to explain the coloration differences. We hypothesized that the differences between the forms were due to different patterns or thicknesses of the waxy layer covering the leaves.

METHODS—Distribution information for the green, silver and intermediate forms of *Serenoa repens* was determined from the herbarium collections of the University of South Florida (USF), University of Florida (UF) and Florida State University (FSU). Determination was subjective, based on the appearance of the dried specimens and/or notes on the labels.

Specimens for microscopic examination were collected from sites in Marion, Jefferson, Brevard, Volusia, and Hillsborough counties, and prepared for both light and scanning electron microscopies, following standard procedures. Old, new and intermediate-aged leaves were collected from each of the three forms. Green and intermediate forms were collected from Brevard County (State Rd. 407, 11 miles west of Kennedy Space Center, on the east side of the road). Additional intermediate forms were collected from two sites in Marion County (State Rd. 40, ¼ mile east of the intersection of SR 40 and 588, and along the Redwater Lake Scenic route off State Rd. 40). The green form was also collected in Hillsborough County from natural populations in the University of South Florida Botanical Garden, Tampa, and in Jefferson County (5 miles from the Marion County line, near 229 mile marker on eastbound Hwy 110). The silver form was collected from Volusia County (off Hwy. A1A, across from the beach near the intersection with Sandpiper Ridge Rd.). An additional cultivated specimen of the silver form was obtained from the University of South Florida Botanical Garden.

RESULTS—Scanning electron micrographs revealed distinct differences in the pattern of epicuticular wax on the leaves of the green and silver forms of *Serenoa repens*. Light micrographs showed no differences in leaf structure. In the green form, epicuticular wax occurs in flat sheets that split and peel up slightly (Fig. 1a), whereas in the silver form, the wax forms in thick patches or blocks of fused rod-like extrusions (Fig. 1b). The latter type of wax is confined to monocots (Barthlott et al., 1998), and is common in other glaucous palms of the genera *Nannorrhops, Copernicia,* and *Hyphaene* (Taylor, unpublished data).

Intermediate forms, which were identified subjectively on the basis of color cast, were more variable. Some had wax layers similar to those of the silver form, whereas others are more like the green form.

DISCUSSION—Clear differences in the epicuticular wax layers of the green and silver forms of *Serenoa repens* suggest a basis for their color differences. The quantity of exfoliating wax in the silver form also suggests a potential for commercial production. Kitzke and Johnson (1975) considered the wax of *Serenoa repens* to have comparable properties, including a 'free-flaking' characteristic that aids in harvesting, to that of the commercial wax palm *Copernicia alba.* They also concluded, however, that the unavoid-

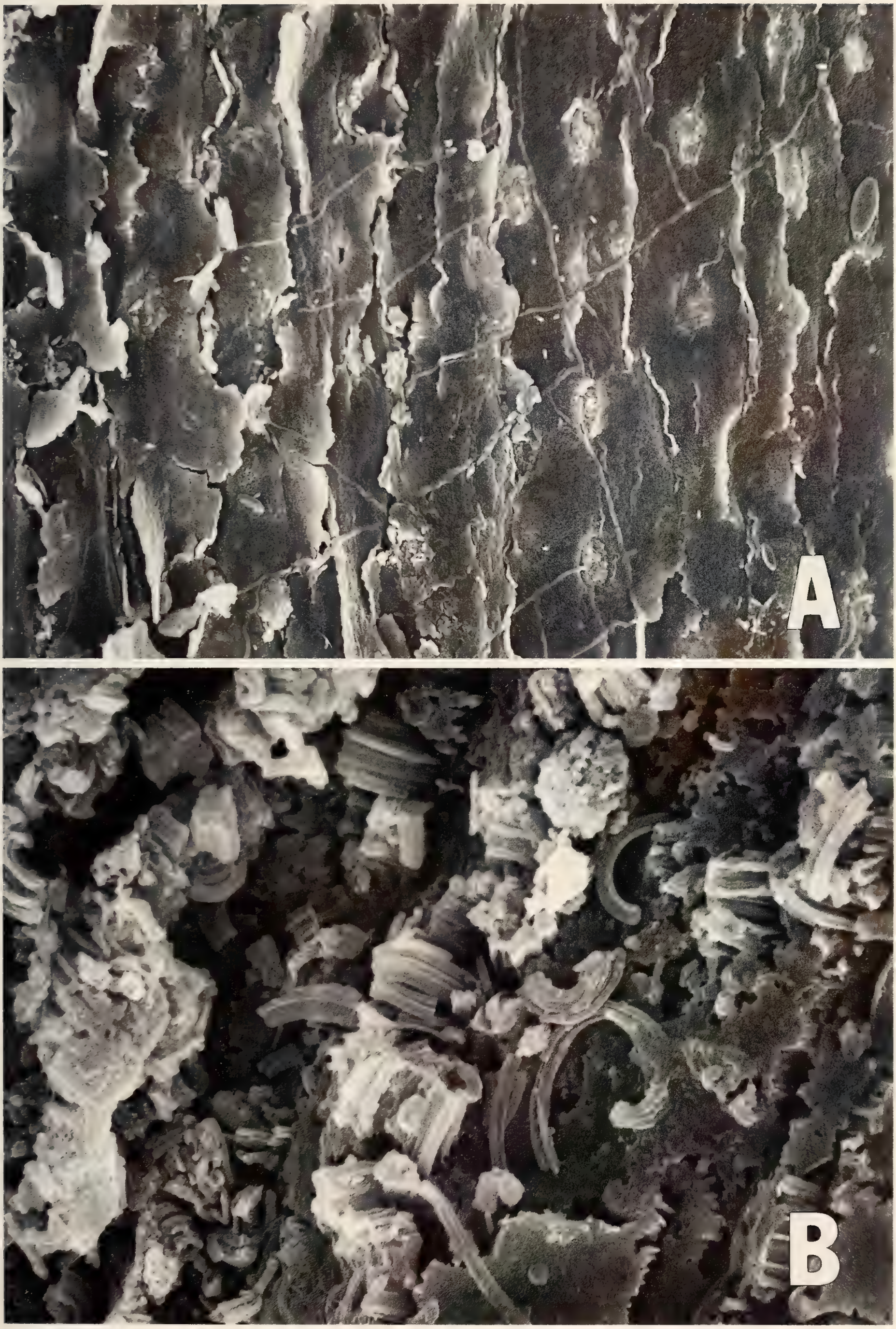

FIG. 1. Scanning electron micrographs of the lower leaf surface of *Serenoa repens* (magnification approximately 400×), showing epicuticular wax patterns: A, green form; B, silver form.

able cost of harvesting *Serenoa* leaves by hand would, in the United States, exceed the market value of the wax.

The distribution of the silver form of *Serenoa repens* along Florida's Atlantic coast and along the ancient coastline of the central ridge, suggests an adaptation to some environmental condition of a coastal habitat. This needs further investigation. The sporadic occurrence of thicker epicuticular wax layers ('intermediate forms') among green populations suggests that the same or different genes controlling this trait are present but rare throughout much of the range of the species.

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WILDLIFE USE OF A CREATED WETLAND IN CENTRAL FLORIDA—*Donald M. Kent*⁽¹⁾ *and Michael A. Langston*⁽²⁾,

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ABSTRACT: *A 31.6 ha (78 acre) created wetland in east central Florida was used by 103 species of wildlife in the first two years following construction. Fauna included nine amphibians, six reptiles, 78 birds, and 10 mammals. Amphibians, birds, and mammals were observed in the first week of the first sampling period, and reptiles were first observed six months later. Cumulative species richness increased throughout the study. Both wetland and upland species were observed.*

DATA on wildlife use of created wetlands are accumulating (Newling and Landin, 1985; Burney et. al., 1989; Hupalo, 1990; Leschisin et al., 1992; Delphey and Dinsmore, 1993; Marcus and Smith, 1993), but the present amount of information still limits our understanding of wildlife use of constructed wetlands. Here we describe wildlife use of a created wetland for a two-year period, beginning immediately upon completion of construction.

The study was conducted in Lake Buena Vista, Orange County, east central Florida, United States. Construction of the 31.6-ha (78 acres) created wetland was completed during the first week of July 1992, and included planting of herbaceous and woody species. The pre-existing habitat, created wetland, and surrounding habitats are described in Kent and co-workers (1999). Wildlife was sampled quarterly from 27 July 1992 through 12 August 1994, using diurnal pedestrian transects and perimeter scan sampling, and nocturnal auditory sampling. Recent signs of wildlife, such as nests, tracks, and scat, were also recorded as wildlife observations. Species observed in the created wetland were designated as wetland or upland species based upon recognized affinities in east central Florida (Brown et al., 1989; Myers and Ewel, 1990). Details of the sampling methods are provided in Kent and co-workers (1999).

The created wetland was used by 103 species of wildlife, including nine amphibians, six reptiles, 78 birds, and 10 mammals (see Kent et al., 1999 for a list). Thirty four species of birds, seven species of amphibians, and six species of mammals were observed during the initial sampling event (July 1992). Avian richness continued to increase throughout the study. No new amphibian species were observed until July 1993, and no new amphibian species were observed thereafter. Mammal richness increased gradually and sporadically after July 1992, and no new mammal species were observed after January 1994. Reptiles were not observed in the created wetland until January 1993. Amphibians, reptiles, birds, and mammals have previously been reported as occurring in restored and created wetlands within one to two years (Burney et al., 1989; Hupalo, 1990; Delphey and Dinsmore, 1993; Marcus and Smith, 1993).

Cumulative species richness increased throughout the course of the study. There was a tendency for more new species to be added during sampling events in the first year (8.5 ± s.e. 3.8, n = 4) than in the second year (5.5 ± 1.3, n = 4), and more during October, January and April (8.2 ± 2.6, n = 6) than in July (3.5 ± 0.7, n = 2). Nevertheless, no dynamic equilibrium was apparent. Pragmatically, a dynamic equilibrium cannot occur until vegetative succession is complete, and then only if there is no disturbance to the wetland or surrounding areas.

The created wetland was used by both wetland (n = 69) and upland (n = 34) wildlife species. All amphibian and reptile species observed are normally associated with wetlands. Upland mammals (2 of 10 species) and birds (32 of 78 species) occurred regularly in the created wetland, although individual species occurred irregularly and in low abundance. Wetland use by upland species was greatest during the initial sampling event (32 percent). Upland species may have been exhibiting exploratory behavior, or exploiting unusually droughty conditions during the first month of the study. Excluding the initial event, the percentage of upland species tended to be greater in October, January, and April (22.7 percent, range 17 to 28 percent, n = 6) than in July (15.0 percent, range 14 to 16 percent, n = 2). This created wetland may be a seasonal source of cover and food for upland species.

We hope this article encourages others to conduct studies of wildlife use of created wetlands, and to publish this information. Studies involving multiple wetlands, and concurrent sampling of wildlife in created wetlands and surrounding habitats, would be particularly valuable.

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INFLUENCE OF DISTANCE AND POST-FIRE RECOVERY ON ACCURACY OF HAND-HELD RADIOTELEMETRY IN FORESTED LANDSCAPES IN SOUTHWEST FLORIDA

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Abstract: *We evaluated the influence of post-fire recovery of vegetation (<6 mo., 24–36 mo., and ≥48 mo.) and geometric distance (Dg) between receiver and transmitter on accuracy of locations estimated with hand-held radiotelemetry equipment in pine-dominated habitats in southwest Florida. We defined accuracy as linear error (E) from true location. Accuracy of radiotelemetry estimates was negatively influenced by post-fire recovery of vegetation, but mean E among post-fire recovery treatments did not differ greatly (29–39 m), presumably due to the rapid recovery of fire-adapted vegetation. The influence of Dg on accuracy of estimates was similar to that of post-fire recovery at Dg < 250 m. Median linear error (Em) at Dg of 50–149 m and 150–249 m was 23 and 32 m and produced mean 95% confidence areas of 1.4 and 2.1 ha, respectively. Distance between receiver and transmitter had a pronounced negative effect on accuracy at Dg of 250–351 m, with Em = 122 m and a mean 95% confidence area of 17.2 ha. Our findings confirmed that distance to transmitter is the most important factor influencing accuracy of location estimates when using hand-held telemetry in densely vegetated habitats and, more importantly, that accuracy declines rapidly at Dg > 250 m. Our study does not replace the need for researchers to develop general estimates of accuracy when conducting radiotelemetry studies, but provides information on the approximate levels of accuracy that can be anticipated and of the variables that most influence accuracy when using hand-held equipment in forested habitats in south Florida. The information we provide will assist researchers in designing studies that include equipment and budgets capable of accomplishing study objectives.*

Hand-held radiotelemetry equipment is less expensive and more versatile for use in rugged terrain than either vehicle or tower mounted systems; consequently, it is an attractive option when designing radiotracking studies. Habitat and landscape attributes, such as density of vegetation and topography, have been reported to influence accuracy of radiotelemetry due to signal reflection (Garrott et al., 1986; Kenward, 1987; Lee et al., 1985). Hand-held systems, therefore, warrant consideration of understory vegetation and distance to transmitter as sources of signal error because hand-held antennas are held closer to the ground than mobile or fixed towers and logistical factors restrict antenna size (White and Garrott, 1990). For these reasons, the accuracy attainable with hand-held systems is a concern, particularly in densely vegetated habitats (Hupp and Ratti, 1983; White and Garrott, 1990).

The availability of regional information describing the extent to which different habitats and landscape features influence accuracy of hand-held radiotelemetry would enable researchers to evaluate whether hand-held systems are likely to provide sufficiently accurate data to attain desired research objectives, if different equipment should be used, or if research objectives should be modified. Unfortunately, information on accuracy of hand-held radiotelemetry in different landscapes is scarce (Johnson et al., 1998) and large amounts of money may be spent on radiotelemetry systems that are too inaccurate to achieve desired goals.

In the absence of topographic relief, density of vegetation is presumed to be the major factor influencing accuracy of radiotelemetry in southwest Florida. The two factors that exert the greatest influence on the density of understory vegetation in southwest Florida are type of habitat and history of fire (Abrahamson and Hartnett, 1990). The objectives of our study were to evaluate the effects of post-fire recovery and distance to transmitter on accuracy of locations estimated with hand-held radiotelemetry in pine-dominated habitats of southwest Florida.

METHODS—We conducted this study from 4 February–5 May 1997 on the 10,560-ha Florida Panther National Wildlife Refuge (FPNWR) in Collier County, Florida (Fig. 1). We measured accuracy of hand-held radiotelemetry equipment in forested habitats dominated by south Florida slash pine (*Pinus elliottii* var. *densa*) with an understory of cabbage palm (*Sabal palmetto*), gallberry (*Ilex glabra*), and saw palmetto (*Serenoa repens*). An extensive network of trails and roads subdivides the FPNWR into 52 fire management units (FMU) that range in size from 103–451 ha ($\bar{x}$ = 238 ha). Our study treatment sites were located within 10 FMU encompassing 1,955 ha.

The FPNWR management plan uses prescribed fire to create a mosaic of FMU fire histories across the refuge. We measured the effect of post-fire recovery (<6, 24–36, and ≥48 mo.) and geometric mean distance (Dg) between receiver and transmitter on accuracy of locations determined by triangulation. We used the cover pole method of Griffith and Youtie (1988) to measure the effect of post-fire recovery on cover of understory vegetation 0–2 m above ground. We used Dg to evaluate the effect of distance on accuracy and on the size of confidence areas of estimated locations (Hupp and Ratti, 1983; Zimmerman, 1990). Dg, which was calculated by taking the nth root of the product of n distance values for each receiver-transmitter combination, expresses in a single value the distance between multiple receiver stations and the estimated transmitter location.

We recorded true locations (±1 m) for all transmitters and receiving stations in Universal Transverse Mercator (UTM) coordinates with a Trimble Pro XL Model TDC1 data logger (Sunnyvale, California) global positioning system (GPS) with navigational beacon. In situations where the navigational beacon could not be used, we contacted the Everglades National Park Trimble GPS base station for differential corrections that were used to ensure accuracy of locations. We used Locate II software (Pacer, Inc., Truro, Nova Scotia) to estimate locations of transmitters from triangulation of ≥3 bearings. Locate II uses Lenth's (1981) maximum likelihood estimator (MLE) to estimate transmitter locations and confidence ellipses and to identify transmitter-receiver combinations for which location estimates can not be calculated (outliers).

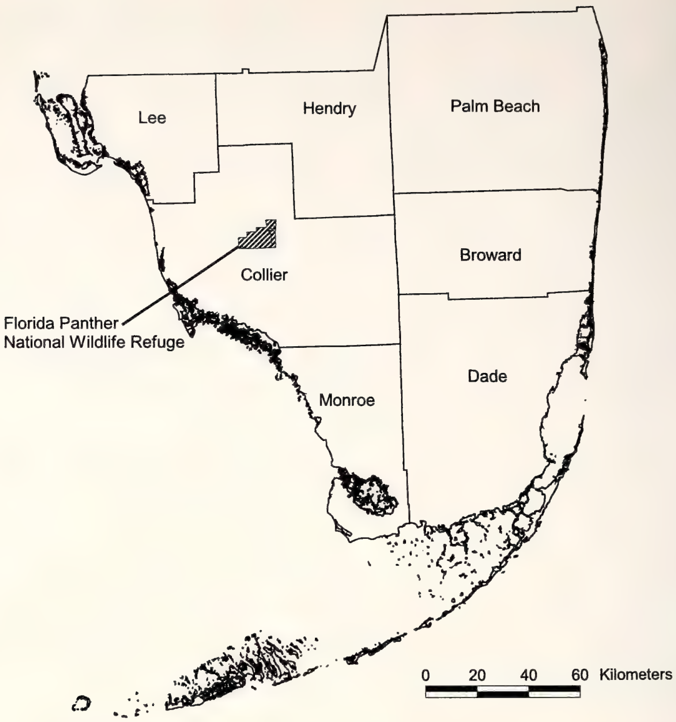

FIG. 1. Location of study area, Florida Panther National Wildlife Refuge, Collier County, Florida.

When outliers were present, the entire set of bearings for that transmitter-receiver combination was removed from analysis.

We estimated transmitter location by triangulation with hand-held compasses (≥3 bearings per location) using Telonics (Mesa, Ariz.) Model TR2 hand-held receivers with headphones and directional 2-element antennas (Model RA-2A). We deployed 44 transmitters (Telonics MOD-505 radiocollars) 1.5 m above the ground and 83.4–241.5 m away from nearby trails where permanent receiving stations were established approximately 150–200 m apart. Two technicians, each of whom had approximately 1-yr. radiotracking experience, worked independently to collect bearings on successive days. Technicians knew neither the location nor the direction of transmitters, and operated from maps of receiving stations and associated transmitter frequencies. Mean linear error between true and estimated transmitter locations did not differ between technicians so data were pooled.

We calculated angle error, the difference between true and estimated bearing, for each bearing (White and Garrott, 1990). Distribution of angle errors was assessed for normality on probability plots and frequency histograms. Data were evaluated for system bias and observer precision, which are defined as mean angle error and standard deviation, respectively (White and Garrott, 1990). We calculated error (E) as the linear distance between true and estimated transmitter location and used E to measure effects of post-fire recovery and Dg on accuracy and precision (Zimmerman and Powell, 1995). Distribution of E is not expected to meet assumptions of normality for parametric statistical analyses because error distances are ≥0 and should be skewed toward smaller values (Zimmerman and Powell, 1995). We log-transformed E and used a Kolmogorov-Smirnov test to test for normality of data (Sokal and Rohlf, 1981). Levene's test (Brown and Forsythe, 1974) was used to test for homogeneity of variances (Sokal

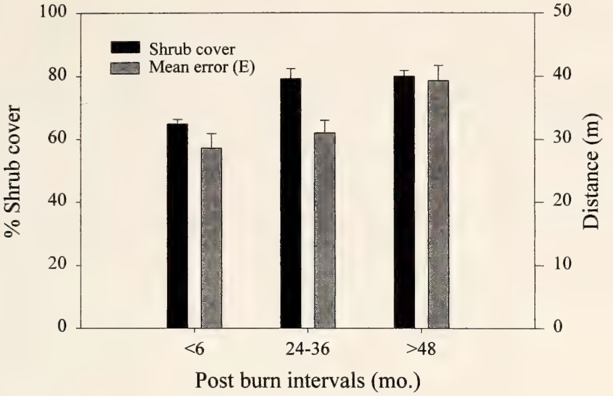

FIG. 2. Influence of post-fire recovery period on percent shrub cover and distance from transmitter to receiver (m) on estimates of mean location error (E) obtained with hand-held radiotelemetry.

and Rohlf, 1981). Parametric statistical analyses were performed only on transformed data that met requirements of normality and homogeneity of variance.

We confirmed dependence of log-transformed E on Dg by simple linear regression and used Dg as a covariant in an analysis of covariance (ANCOVA) to analyze effects of post-fire recovery and Dg on E. ANCOVA adjusts treatment data for differences in the covariant before examining differences due to the treatments themselves (Sokal and Rohlf, 1981). Because the linear relationship between Dg and accuracy was weak, we created 6 categories of Dg in 50-m intervals (50–351 m) to evaluate whether accuracy was influenced differently among distance categories. We used box-and-whisker plots to identify and pool distance categories that were statistically similar and, because linear error variances were different among the six distance categories (Levene's test: $F = 27.5$, df = 5, 380 df, $P < 0.01$), we compared median E (Em) values among distance categories with a nonparametric Kruskal-Wallis test. We used Statgraphics Plus 2.1 software (Manugistics Inc., Rockville, Maryland) to conduct statistical analyses.

RESULTS—We recorded 385 (85.6%) usable locations from 450 triangulation attempts ($n \geq 3$ bearings/triangulation) for 44 transmitters. Mean angle error, calculated by MLE, was −3.5° ($s = 18.1°$). Mean percent cover of understory vegetation was 0.69, 0.79, and 0.80 at <6, 24–36, and ≥48 mo., respectively. Both cover of woody understory vegetation (simple linear regression: $F = 45.0$, df = 1, 302, $P < 0.01$) and E increased ($F = 3.61$, df = 2, 382, $P = 0.03$) as post-fire recovery progressed (Fig. 2). The effective change in mean E over time post-fire recovery ranged from 29–39 m (Fig. 2). Accuracy of radiotelemetry estimates (E) was also negatively influenced by increasing Dg ($F = 37.8$, df = 1, 385, $P < 0.01$). Linear regression revealed a significant ($F = 78.2$, df = 1, 385, $P < 0.01$) but weak correlation ($r = 0.41$) between E and Dg. We found significant differences among Dg intervals of 50 m (Kruskal-Wallis test = 71.1, df = 5, $P < 0.01$). We used box and whisker plots to identify and pool similar Dg intervals to form new intervals of 50–149 m (median = 115 m, $n = 280$), 150–249 m (median = 179 m, $n = 195$), and 250–351 m (median = 287 m, $n = 20$). Median linear error (Em) was similar between Dg of 50–149 m (Em = 23.4

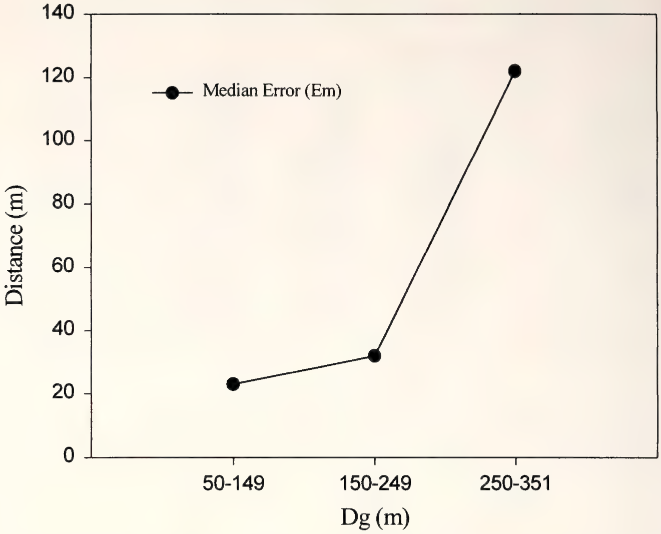

FIG. 3. Influence of geometric distance (Dg) on median location error (Em) of locations estimated with hand-held radiotelemetry ($s^2 \leq 0.1$ for all Em estimates).

m, $s^2 = 0.12$) and 150–249 m (Em = 32.0 m, $s^2 = 0.10$), and increased rapidly at Dg of 250–351 m (Em = 122.4 m, $s^2 = 0.05$)(Fig. 3). Corresponding 95% confidence areas followed a similar pattern, with mean 95% confidence areas of 1.4 and 2.1 ha for Dg of 50–149 and 150–249 m, and 17.2 ha at distances 250–351 m.

DISCUSSION—Researchers are often faced with making difficult decisions on how to allocate limited budgets to accomplish research objectives. Hand-held radiotelemetry is often a cost-efficient approach to conducting radiotracking studies if the accuracy of location estimates is sufficient to achieve research objectives. The single most important factor influencing the accuracy of locations estimated with hand-held equipment in our study was distance from receiver to transmitter. More importantly, we found that median E associated with location estimates was relatively similar at Dg intervals of 50–149 m and 150–249 m, but increased rapidly at Dg of (250–351 m) (Fig. 3). The 95% confidence areas produced at Dg < 250 m were approximately 2 ha, which is an acceptable size for estimating patterns of habitat use and movement of mobile species in most landscapes. The 95% confidence areas produced at Dg of 250–351 m, however, were approximately 17 ha and would preclude evaluation of habitat preferences in most circumstances. Density of vegetation increased over time during post-fire recovery and also influenced accuracy of estimates (Fig. 2), but the effect of vegetation was relatively minor compared to the effects of distance. The relatively minor differences observed in accuracy among post-fire recovery periods was presumably due to signal interference from standing trees and the rapid recovery of fire-adapted vegetation such as cabbage palm and saw palmetto.

Several factors can influence the accuracy of estimated locations obtained using radiotelemetry, such as observer skill, precision, and the interior angle generated by the location of the receiver during successive bearings. These and other aspects of radiotelemetry are discussed in detail in White and Garrott (1990) and are beyond the scope of this paper. The purpose of this study was to provide information that would be useful to resource managers and researchers in determining whether hand-held radiotelemetry equipment would likely be able to provide sufficiently accurate information to achieve research objectives in densely forested habitats.

We determined distance was the most important factor influencing accuracy and that accuracy of estimates declined rapidly at Dg > 249 m (Fig. 3). Detailed discussions on how increasing distance between transmitter and receiver influences accuracy of radiotelemetry is provided elsewhere (Hupp and Ratti, 1983; White and Garrott, 1990). Dg and arithmetic means are approximately equal when bearing distances between transmitter and receiver are similar (e.g., bearing distances of 200, 250, and 300 m have a Dg of 247 m and an arithmetic mean of 250 m). Consequently, to obtain data with 95% confidence areas of approximately 2 ha requires that researchers obtain average bearing distances of ≤250 m. Researchers considering using hand-held radiotelemetry in densely vegetated habitats, therefore, need to evaluate whether they will, on average, be able to obtain bearings of ≤250 m between receiver and radiotagged animals if their objectives include making meaningful predictions about habitat preferences and localized movement patterns.

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INVENTORY OF FISHES OF EVERGLADES NATIONAL PARK

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Abstract: *This inventory of the fishes of Everglades National Park summarizes the ichthyological and fisheries investigations that have provided information on the composition and distribution of the park's marine, brackish and freshwater fish faunas. Descriptions of the major aquatic habitats of the park provide a context for the subsequent complete inventory for the area. South Florida is a region in which members of the Antillean and Carolinian fish faunas meet and mix, giving rise to a diverse assemblage of fishes. Two hundred and ninety species of fishes have been recorded from the park, the majority of which occur both in North American and tropical West Atlantic waters. All of the native freshwater fishes in the park are derived from temperate North America; conversely, the seven established non-indigenous fish species originated in tropical waters. The table of species includes abundance and habitat use information. Species that are of hypothetical or questionable occurrence are also noted.*

Everglades National Park is a 0.9 million-hectare wilderness established at the southern tip of the Florida peninsula in 1947. On the north, the park is bordered by the Water Conservation Areas, by Big Cypress National Preserve on the west, by the developed coastal ridge to the east, and it extends to the mangrove-lined coasts of southern Florida (Fig. 1). Much of Florida Bay is within the southern park boundaries, which follow the inside alignment of the upper and middle Florida Keys. The congressionally authorized expansion area brings the park boundary to include northeast Shark Slough. Upland and wetland habitats comprise the freshwater and saline glades of the park. The park also includes one of the most extensive mangrove swamps on earth.

The scientific literature describing the composition and distribution of the southern Florida fish fauna began with the works of Henshall (1891), Lönnberg (1894), and Evermann and Kendall (1900). Until the middle of this century, relatively little was known about the fishes of the area included within Everglades National Park, although Schroder (1924) discussed the fishing industry that operated around Cape Sable early in this century. Kilby and Caldwell (1955) and Carr and Goin (1955) presented distributional data on Everglades freshwater and euryhaline fishes, and Briggs (1958) summarized the distribution of all Florida fishes.

Following those general faunal surveys, a number of important marine studies were completed within the park. Tabb and Manning (1961), Tabb

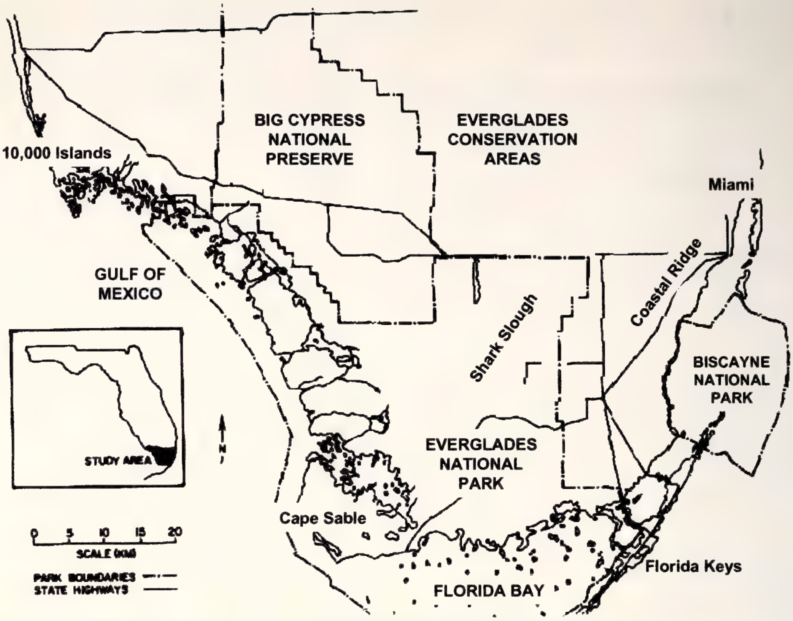

FIG. 1. Extreme southern Florida showing the boundaries of Everglades National Park and important landscape features.

and Roessler (1989), and Tabb and co-workers (1962; 1974) discussed the ecology and distribution of estuarine and marine fishes in Everglades National Park. Odum (1971) described the occurrence and food habits of fishes in North River, and McPherson (1970) listed the fishes taken in the Shark River estuary. Dahlberg (1970) and Daly (1970) discussed the menhaden and anchovies, respectively, of the park waters. Other works on marine and estuarine species included: Hudson and co-workers (1970) and Schmidt (1979) on the Florida Bay fauna, Roessler (1970) on Buttonwood Canal fishes, Clark (1971), Davis and Hilsenbeck (1974), and Schmidt (1993) on Whitewater Bay/Shark River species, and Jannke (1971) on sciaenid fishes in Everglades National Park. The decade of the 1980s produced numerous data on marine fishes from Florida Bay and the Gulf of Mexico by Colby and co-workers (1985), Powell and co-workers (1987), Robblee and Hutinet (1987), Rutherford and co-workers (1986), Sogard and co-workers (1989a; 1989b), and Thayer and co-workers (1987). The marine ichthyoplankton of the park was described by Collins and Finucane (1984), and A. Powell and co-workers (1987). Papers presented at the 1987 Florida Bay Symposium and published in Volume 50(1) of the Bulletin of Marine Science (1989) comprised the most complete body of data on the biology and fishery harvest of game species in the park. In recent years several papers have presented information about fishes inhabiting mangrove creeks and flats along the northern shores of Florida Bay (Ley, 1992; McIvor et al., 1994; and Lorenz, 1997).

Research in areas adjacent to the park included the survey by Lindall and co-workers (1973) of the inshore and offshore fishes of the Gulf of Mexico, the study by Carter and co-workers (1973) of the fishes of the Ten Thousand Islands, and recent unpublished collections by John Briggs and students from the Ten Thousand Islands (Tolley, 1983), and by a National Marine Fisheries Service cruise in the Gulf of Mexico (Burgess, 1983).

Historically, considerably less research has been focused upon freshwater fish communities in the park. The most comprehensive studies were those by Kushlan and Lodge (1974) and Loftus and Kushlan (1987), which thoroughly documented the status and distribution of fishes in the fresh waters of the park and its surroundings. Courtenay and co-workers (1974) and Shafland (1996) described the occurrence of non-native freshwater fishes in and near the park. Loftus and Kushlan (1987) clarified and revised those data, and Loftus (1987, 1988) and Courtenay (1997) added information on recently established non-native species. The fishes of the Everglades Water Conservation Areas immediately north of the park have been recorded by Dineen (1984) and Trexler and Jordan (1999). Several species that occur north of the park have never been collected within the park (Dineen, 1984; Loftus and Kushlan, 1987). Additional information on the relative species abundance and densities of fishes in and near the park may be found in Loftus and Eklund (1994), Howard and co-workers (1995), and Trexler and co-workers (1996).

Paulson (1959), Phillips (1971), and Schmidt (1975) have compiled previous fish lists for Everglades National Park. Extensive bibliographies for the marine fauna may be found in Schmidt (1991) and Schmidt and Kayer (1979), and for the freshwater ichthyofauna in Kushlan and Lodge (1974) and Loftus and Kushlan (1987).

This updated inventory of the ichthyofauna of the park contains an additional 70 species since the last list was compiled (Schmidt, 1975). This reflects the more complete knowledge of the fishes that has resulted from the increasing number of research studies in the aquatic habitats of the park because of Everglades restoration efforts and the seagrass dieoff phenomenon (Robblee et al., 1991).

METHODS—This latest inventory of Everglades fishes has been compiled from several sources. Previous checklists for the park (Paulson, 1959, Phillips, 1971, and Schmidt, 1975) provided much of the background information for this inventory. In a few cases of incomplete documentation for a species listed in earlier checklists, I decided to keep the record if the regional literature supported its inclusion here. Records from the checklists were supplemented by the many published studies on the local freshwater and marine ichthyofaunas that included information on the habitat occurrence and abundance of various species. Examination of accession records at the three museums that housed the most extensive collections of park fishes, the University of Miami Rosenstiel School of Marine and Atmospheric Sciences (UMML—collection now at UF), the Florida Museum of Natural History (UF), Gainesville, and the

Everglades National Park museum (EVER) provided several unpublished records. Finally, the experiences of the author and, in particular, personal communications with colleagues were invaluable in preparing this latest inventory.

I have reported all fishes presently documented from park waters. The main inventory table includes information on the relative abundance and habitat occurrences of each species. Introduced (non-native) species are so designated in the table. The reference to the authority for the presence of a species in the park is also noted. Common and scientific names generally follow those in Robins and co-workers (1991). In a second table, fishes that have been taken from nearby waters outside the park, in habitats that also occur within the park, are listed as species of hypothetical occurrence. Those species may be found in the park with time or with further collecting. In a separate table, I have listed species of doubtful occurrence, the presence of which in park waters is uncertain due to the absence of voucher specimens, or to distributional anomalies.

The fishes are classified either as marine, estuarine, or freshwater, based upon the salinity in which they usually occur. Fishes (euryhaline species) that tolerate a range of salinities are so noted in the table. Aquatic habitats within the park are varied; descriptions of the major types follow:

Freshwater everglades—A mosaic of aquatic plant communities combine to form the habitat that covers much of the park's interior. Natural habitats include sawgrass marshes, which cover the most area of the freshwater Everglades, and are dominated by *Cladium jamaicense.* Those habitats are interspersed with wet prairie and slough communities composed of various aquatic plant genera (e.g., *Nymphaea, Panicum, Eleocharis,* and *Rhynchospora*). The floating species of *Utricularia* support luxuriant surface mats of periphyton. Alligator ponds provide open, deep-water habitat for much of the year and provide refuge for fishes during the dry season when the surrounding shallow marshes dry. Along the edges of the main Everglades marshes, seasonally inundated prairies of *Muhlenbergia* grass, studded by numerous limestone solution holes, provide habitat for fishes. A limited area of cypress swamp (*Taxodium* spp.) also is present within the park.

Created freshwater habitats are present in and near the park. Canals and borrow pits are artificial deep-water habitats constructed for drainage, levee fill, or mining operations and are anthropogenic analogs, albeit larger and deeper, to alligator ponds. Canals have replaced all natural drainages of any significance along the extreme southeastern coast of Florida (Beck, 1965). Canals through the Everglades usually are bordered on one side by natural aquatic habitats and on the other side by a levee or road. The sloping canal edges are lined by marsh or swamp vegetation, particularly sawgrass, willow, or cattail (*Typha* spp.). Submerged vegetation is abundant along the margins of these canals. More detailed descriptions of freshwater habitats and their water quality characteristics may be found in Loftus and Kushlan (1987) and Gunderson and Loftus (1993).

Estuarine habitats—These occur seaward of the interior freshwater marshes in an area referred to as the mangrove zone. These habitats include seasonally freshwater rivers, creeks, and ponds bordered by red mangrove (*Rhizophora mangle*). Sawgrass, black rush (*Juncus roemerianus*), and dwarf mangroves occur in marshes between the channels and ponds. Typical submerged plants in this region include *Najas guadalupensis* and *N. marina, Utricularia* spp., *Chara* spp., and *Ruppia maritima.* A series of large lakes and bays inland from the coast (e.g., Whitewater and Coot bays, Alligator Bay, West, Bear, Fox, and Cuthbert lakes) form extensive estuarine habitats.

During severe dry seasons, the watercourses become brackish or saline along their entirety. As salinity gradients change seasonally, fishes move up and down the rivers in response. The channels and deeper ponds offer dry season refuge for fishes from the surrounding areas. Fishes trapped in the drying marshes and shallow ponds become prey for many species of wading birds. The physical and biological characteristics of this region are more fully described by Odum and co-workers (1982) and Gilmore and Snedaker (1993).

Marine habitats—These are found in Florida Bay and the Gulf of Mexico and range from shallow carbonate banks and mudflats to deep channels. Large flats are covered by grassbeds of the genera *Thalassia, Halodule,* and *Syringodium,* with a variety of associated algae. The shorelines are edged by red and black mangroves, buttonwood (*Conocarpus erectus*), and by coastal prairies in some areas. A large number of islands (keys) in Florida Bay provide additional shallow shoreline habitat. Oyster bars composed of living and dead *Crassostrea virginica* provide hard-bottom habitat along some sections of coastline. Sandy beaches and sand substrates are generally uncommon. Reef-building corals are mostly absent, although areas of soft corals exist in southern Florida Bay. Tidal amplitude in much of Florida Bay is rather small; the effects of wind-driven water often overwhelm or enhance tidal influences. Detailed descriptions of marine environments in the park and their characteristic biota may be found in Tabb and Manning (1961), Tabb and co-workers (1962), Thayer and co-workers (1987), G. Powell and co-workers (1987), and Robblee and co-workers (1991).

Relative abundance categories used in this inventory are: *Common,* numerous and ubiquitous in appropriate habitats; *Locally Common,* numerous at specific locations or microhabitats but rare or absent in other parts of habitat; *Uncommon,* present in small numbers in suitable habitat or only locally or seasonally numerous; *Rare,* present only in very small numbers and of irregular occurrence, or occurs only in small, localized populations. These abundance categories apply only within park waters. Abundances of many species may differ greatly outside of the park, usually because of habitat and physico-chemical differences.

RESULTS AND DISCUSSION—Southern Florida is an area in which members of the Antillean and Carolinian faunas meet. The fishes in the park belong to 22 orders and 85 families. Of the 290 native species of fishes reported from Everglades National Park (Table 1), 83 have strictly North American distributions. Florida is the northern limit for an additional 35 species of mainly neotropical fishes that occur in the park. The majority of fishes (173 species) found in Everglades National Park are found both in North American (not limited to Florida waters) and neotropical waters. Twenty-nine species listed as hypothetical have not been collected from park waters but occur in habitats shared by the park (Table 2). Some of those species may be found in the park with more extensive sampling or, in the case of the non-native species, may colonize by moving through the canal system where they presently reside to the east. Eleven species recorded from the area of the park are regarded as species of questionable occurrence, either because the record is far outside of the usual range for that species and/or because there are no voucher specimens with which to confirm the identification (Table 3).

All strictly freshwater fishes native to southern Florida are derived from North American temperate waters; most of these species range widely along the southeastern coastal plain (Loftus and Kushlan, 1987). Primary freshwater species (those groups completely restricted to fresh water) within the park number 20, while those that tolerate some salinity (secondary freshwater species) number eight. Of these freshwater species, most belong to two families of Perciformes: Centrarchidae and Cichlidae. All species of cichlids are introduced here. Both families have species that tolerate saline conditions and occasionally enter upper estuarine waters. In the densely vegetated marshes, members of the Cyprinodontidae, Fundulidae, and Poe-

TABLE 1. Fish relative abundance by habitat in Everglades National Park. Habitat descriptions are provided in the text. (I) = Introduced species; (FW) indicates a species found also in the freshwater reaches of the estuary.

Scientific name	Natural FW	Created FW	Estuarine	Marine	Citation*
Ginglymostomatidae					
Ginglymostoma cirratum				R	1, 2
Rhincodontidae					
Rhincodon typus				R	21
Lamnidae					
Carcharodon carcharias				R	7
Isurus oxyrinchus				R	2, 10
Carcharhinidae					
Carcharhinus leucas			U (FW)	U	3, 11
Carcharhinus limbatus			LC	LC	1, 4, 7
Carcharhinus plumbeus				R	7
Galeocerdo cuvier				R	7
Negaprion brevirostris				LC	2, 14
Rhizoprionodon terraenovae				C	14
Sphyrnidae					
Sphyrna lewini				R	2
Sphyrna mokarran				R	2
Sphyrna tiburo			LC	LC	1, 2
Pristidae					
Pristis pectinata			LC	LC	1, 2
Rhinobatidae					
Rhinobatos lentiginosus				R	5
Torpedinidae					
Narcine brasiliensis				R	5
Rajidae					
Raja laevis				R	7
Dasyatidae					
Dasyatis americana			LC	LC	1, 4
Dasyatis sabina			U (FW)		3, 11
Gymnura micrura			R	R	22
Myliobatidae					
Aetobatus narinari				R	2
Rhinoptera bonasus				U	7, 14
Mobulidae					
Manta birostris				R	7
Lepisosteidae					
Lepisosteus platyhincus	LC	C	LC		1, 3
Amiidae					
Amia calva	U	C	LC (FW)		3

TABLE 1. Continued.

Scientific name	Natural FW	Created FW	Estuarine	Marine	Citation*
Elopidae					
Elops saurus			C (FW)	C	1, 3
Megalops atlanticus		LC	LC (FW)	LC	1, 3
Albulidae					
Albula vulpes			U	U	3
Anguillidae					
Anguilla rostrata	C	C	C (FW)		3, 6
Muraenidae					
Gymnothorax moringa				R	1
Gymnothorax nigromarginatus				U	1
Ophichthidae					
Ahlia egmontis			C	C	1
Bascanichthys bascanium				C	1, 5
Bascanichthys scuticaris				C	1
Myrophis punctatus			LC	LC	1, 4
Ophicthus gomesi			C	C	1, 2
Clupeidae					
Brevoortia patronus				R	2, 12
Brevoortia smithi			LC	LC	1
B. patronus x B. smithi				U	4
Dorosoma petenense		LC	R		3
Harengula humeralis			LC	R	4, 6
Harengula jaguana				C	1, 2, 4
Jenkinsia lamprotaenia				U	6
Opisthonema oglinum			C	C	2, 4
Sardinella aurita				U	4, 6
Sarinella brasiliensis				R	8
Engraulidae					
Anchoa cubana				R	1, 2
Anchoa hepsetus				C	1, 4, 5
Anchoa lamprotaenia				R	4
Anchoa mitchilli			C (FW)	C	1
Anchoviella perfasciata				R	2
Cyprinidae					
Notemigonus crysoleucas	U	LC			3
Notropis maculatus	R	R			3
Notropis petersoni	C	C	LC (FW)		3
Catostomidae					
Erimyzon sucetta	LC	C			3
Ictaluridae					
Ameiurus natalis	C	U	LC (FW)		3
Ameiurus nebulosus	R	U			3
Ictalurus punctatus		U			3
Noturus gyrinus	LC	LC	LC (FW)		1, 3

TABLE 1. Continued.

Scientific name	Natural FW	Created FW	Estuarine	Marine	Citation*
Clariidae					
Clarias batrachus (I)	U	LC	LC (FW)		3
Ariidae					
Arius felis			C (FW)	C	1, 3
Bagre marinus			LC (FW)	LC	3, 4
Esocidae					
Esox niger		LC/R			3
Synodontidae					
Synodus foetens			C	C	2, 4
Trachinocephalus myops				R	7
Ophidiidae					
Ophidion grayi				U	5
Ophidion holbrooki				R	5
Ophidion welshi				R	5
Bythitidae					
Gunterichthys longipenis				R	6
Ogilbia cayorum				R	22
Batrachoididae					
Opsanus beta			C	C	1, 4
Porichthys plectrodon			U	U	4
Antennariidae					
Histrio histrio				R	4, 8
Ogcocephalidae					
Ogcocephalus nastutus			R	R	4
Ogcocephalus radiatus				U	2, 5
Gobiesociade					
Gobiesox strumosus				U	1, 2
Exocoetidae					
Chriodorus atherinoides				LC	1, 2
Hemiramphus balao				R	6
Hemiramphus brasiliensis			LC	LC	1
Hyporhamphus unifasciatus			C	C	1, 4
Prognichthys gibbifrons				R	4
Belonidae					
Strongylura marina			LC (FW)	LC	4
Strongylura notata			C (FW)	C	1, 2, 4
Strongylura timucu			C (FW)	C	1, 3, 8
Tylosurus crocodilus				R	2, 8
Aplocheilidae					
Rivulus marmoratus			LC (FW)		1, 4, 10

TABLE 1. Continued.

Scientific name	Natural FW	Created FW	Estuarine	Marine	Citation*
Cyprinodontidae					
Cyprinodon variegatus	LC		C (FW)	C	1, 2, 3, 8
Floridichthys carpio			C (FW)	C	2, 3, 6, 8
Jordanella floridae	LC	LC	C (FW)		3, 10
Fundulidae					
Adinia xenica	U		LC (FW)		1, 3
Fundulus chrysotus	C	U	U (FW)		3
Fundulus confluentus	C		C (FW)		1, 3
Fundulus grandis			C (FW)	C	1, 2, 3, 5
Fundulus seminolis	U				3, 6
Fundulus similis		LC	LC (FW)	LC	1, 2, 3
Lucania goodei	C		U (FW)		3
Lucania parva		C	C (FW)	C	2, 3
Poeciliidae					
Belonesox belizanus (I)	C	C	C (FW)		3
Gambusia holbrooki	C	C	LC (FW)	LC	1, 3
Gambusia rhizophorae			U (FW)		3
Heterandria formosa	C	C	U (FW)		3
Poecilia latipinna	LC	LC	LC (FW)	LC	1, 2, 3
Atherinidae					
Atherinomorus stipes					2, 6
Hypoatherina harringtonensis					6
Labidesthes sicculus	U	LC			3
Membras martinica			R	C	4, 5, 6
Menidia beryllina			C (FW)		3, 4
Menidia peninsulae				LC	6
Syngnathidae					
Anarchopterus criniger				LC	2
Bryx dunckeri				LC	1, 2
Cosmocampus albirostris				R	2
Hippocampus erectus			LC	LC	1, 4
Hippocampus zosterae				C	1, 4
Micrognathus crinitus				U	21
Syngnathus floridae				C	4
Syngnathus louisianae				LC	4, 5
Syngnathus scovelli			LC	LC	1, 4
Scorpaenidae					
Scorpaena albifimbria				R	2 (U)
Scorpaena brasiliensis				U	1, 5
Triglidae					
Bellator egretta				R	1
Prionutus ribo				R	10
Prionotus scitulus				LC	5, 13
Prionotus tribulus			LC	LC	1, 2, 4

TABLE 1. Continued.

Scientific name	Natural FW	Created FW	Estuarine	Marine	Citation*
Centropomidae					
Centropomus parallelus	R		R (FW)		9
Centropomus pectinatus	R		U (FW)	U	8
Centropomus undecimalis		C	LC (FW)	LC	3, 9
Serranidae					
Centropristis striata				R	5
Diplectrum bivittatum				R	8
Diplectrum formosum				LC	2, 4
Epinephelus itajara				LC	4, 11
Epinephelus morio			LC (FW)	U	1
Epinephelus striatus				R	1, 2
Hypoplectus unicolor				U	2, 5
Mycteroperca bonaci				R	2
Mycteroperca microlepis				LC	1
Rypticus maculatus				R	22
Centrarchidae					
Elassoma evergladei	LC	LC	LC (FW)		3
Enneacanthus gloriosus	U	C			3
Chaenobryttus gulosus	C	C	U (FW)		3
Lepomis macrochirus	U	C	U (FW)		3
Lepomis marginatus	C	C			3
Lepomis microlophus	U	C	U (FW)		3
Lepomis punctatus	C	C	U (FW)		3
Micropterus salmoides	U	LC	LC (FW)		3
Pomoxis nigromaculatus		R			3
Percidae					
Etheostoma fusiforme	R	LC	R (FW)		3
Priacanthidae					
Priacanthus arenatus				R	2
Apogonidae					
Astrapogon alutus				U	5
Pomatomidae					
Pomatomus saltatrix				R	2, 8
Rachycentridae					
Rachycentron canadum				U	2, 4
Echeneidae					
Echeneis naucrates			U	U	1, 4
Echeneis neucratoides				U	2
Carangidae					
Caranx bartholomaei			R	R	2
Caranx crysos				U	1, 2
Caranx hippos			C (FW)	C	1, 2, 3
Caranx latus				R	8
Caranx ruber				R	7

TABLE 1. Continued.

Scientific name	Natural FW	Created FW	Estuarine	Marine	Citation*
Chloroscombrus chrysurus				U	1, 2, 4
Hemicaranx amblyrhynchus				R	4
Oligoplites saurus			LC (FW)	LC	1, 2, 4
Selene setapinnis			LC	R	2
Selene vomer				LC	2, 4
Seriola dumerili				R	7
Seriola zonata				R	7
Trachinotus carolinus				U	2, 8
Trachinotus falcatus				U	2, 8
Coryphaenidae					
Coryphaena hippurus				R	22
Lutjanidae					
Lutjanus analis				R	2
Lutjanus apodus			U	U	2
Lutjanus griseus			C (FW)	C	1, 2, 3
Lutjanus jocu			C	C	1
Lutjanus synagris			LC	LC	1, 4
Ocyurus chrysurus				R	2
Lobotidae					
Lobotes surinamensis				U	2, 4
Gerreidae					
Diapterus plumieri			C (FW)	C	1, 2, 3, 4
Eucinostomus argenteus			C (FW)	C	4, 11
Eucinostomus gula			C (FW)	C	3, 4
Eucinostomus harengulus				R	10 (PC)
Eucinostomus lefroyi			U	U	21
Gerres cinereus			LC	LC	1, 2
Haemulidae					
Anisotremus virginicus				R	1, 2
Haemulon aurolineatum			U	U	1, 2
Haemulon chrysargyreum				R	8
Haemulon flavolineatum				R	6
Haemulon parra				U	2
Haemulon plumieri			C	C	1, 2, 6
Haemulon sciurus				U	1, 7, 9
Orthopristis chrysoptera			C	C	1, 2, 5
Sparidae					
Archosargus probatocephalus			LC (FW)	LC	1, 2, 3
Archosargus rhomboidalis				U	2
Calamus arctifrons				LC	1
Calamus leucosteus				R	6
Calamus penna				R	22
Lagodon rhomboides			C	C	1, 2, 8
Sciaenidae					
Bairdiella batabana				U	2, 4
Bairdiella chrysoura			C (FW)	C	1, 2, 6, 11

TABLE 1. Continued.

Scientific name	Natural FW	Created FW	Estuarine	Marine	Citation*
Cynoscion arenarius			U	U	4
Cynoscion nebulosus			LC	LC	1
Equetus acuminatus				R	2
Equetus lanceolatus				R	1
Equetus umbrosus				U	5
Larimus fasciatus				R	7
Leiostomus xanthurus			U	U	1, 5
Menticirrhus americanus				LC	2, 5
Menticirrhus littoralis				U	2
Menticirrhus saxatilis				U	17
Micropogonias undulatus				R	1, 4
Pogonias cromis			U	U	1, 4, 8
Sciaenops ocellatus			LC (FW)	LC	1, 3
Stellifer lanceolatus				R	17
Ephippidae					
Chaetodipterus faber				C	1, 2, 4, 5
Pomacanthidae					
Holacanthus ciliaris				R	16
Cichlidae					
Astronotus ocellatus (I)		C			3, 15
Cichla ocellaris (I)		R			21
Cichlasoma bimaculatum (I)	LC	LC			3
Cichlasoma urophthalmus (I)	C	C	U (FW)		15
Oreochromis aureus (I)	LC	C	LC (FW)		3, 15
Oreochromis mossambicus (I)		U			18
Tilapia mariae (I)	U	U	U (FW)		3
Mugilidae					
Agonostomus monticola			R		11
Mugil cephalus		U		C	1, 2, 3, 8
Mugil curema			R	C	1, 2, 8
Mugil gyrans			C (FW)	C	2, 5
Sphyraenidae					
Sphyraena barracuda			U (FW)	LC	1, 2, 8, 13
Sphyraena guachancho				R	6
Polynemidae					
Polydactylus octonemus				U	7, 10
Pomacentridae					
Abudefduf saxatilis				R	7
Pomacentrus leucostictus				R	7
Labridae					
Bodianus rufus				R	12
Halichoeres bivittatus				R	7
Lachnolaimus maximum				U	1, 4

TABLE 1. Continued.

Scientific name	Natural FW	Created FW	Estuarine	Marine	Citation*
Scaridae					
Cryptotomus roseus				R	6
Nicholsina usta				LC	1, 5, 6
Scarus guacamaia				R	7
Scarus taeniopterus				R	2
Sparisoma aurofrenatum				R	2
Sparisoma chrysopterum				R	2
Sparisoma radians				R	13
Sparisoma rubripinne				U	1, 2, 4
Sparisoma viride				R	2, 22
Clinidae					
Paraclinus fasciatus				U	6, 8
Paraclinus marmoratus				U	6, 8
Blenniidae					
Chasmodes saburrae				LC	1, 2
Hypsoblennius hentz			LC (FW)	R	1
Parablennius marmoreus				R	1, 5
Callionymidae					
Diplogrammus pauciradiatus				LC	2, 6
Eleotridae					
Dormitator maculatus			LC (FW)		1, 4
Eleotris pisonis			R		4
Gobiomorus dormitor			R (FW)		3
Gobiidae					
Barbulifer ceuthoecus				R	8
Bathygobius soporator			LC	U	20
Coryphopterus glaucofraenum				R	16
Gobionellus oceanicus			U	U	4
Gobionellus saepepallens				R	8
Gobionellus shulfeldti				R	9
Gobionellus smaragdus			LC (FW)	LC	4
Gobiosoma bosc			LC (FW)	U	2, 3
Gobiosoma robustum			C	C	1
Lophogobius cyprinoides			LC (FW)	LC	1, 3
Microgobius gulosus			C (FW)	U	1, 2, 3
Microgobius microlepis				U	2, 6
Microgobius thalassinus			R	R	9, 13
Microdesmidae					
Microdesmus sp.				R	19
Acanthuridae					
Acanthurus chirugus				R	6
Scombridae					
Scomberomorus cavalla				R	2, 4
Scomberomorus maculatus				LC	1
Scomberomorus regalis				R	7

TABLE 1. Continued.

Scientific name	Natural FW	Created FW	Estuarine	Marine	Citation*
Xiphiidae					
Xiphias gladius				U	7
Stromateidae					
Nomeus gronovii				R	8
Peprilus alepidotus				R	12, 22
Bothidae					
Ancylopsetta quadrocellata				U	1, 5
Bothus ocellatus				R	2
Citharichthys macrops				R	5
Citharichthys spilopterus				LC	4, 12
Etropus crossotus				U	1, 4
Paralichthys albigutta			LC	LC	4, 5
Paralichthys lethostigma				U	1, 2
Paralichthys squamilentus				R	1
Syacium gunteri				LC	12
Soleidae					
Achirus lineatus			C (FW)	C	1, 2, 3, 5
Symphurus diomedianus				U	5
Symphurus plagiusa			C	C	1, 4, 13
Trinectes inscriptus				R	6
Trinectes maculatus			LC (FW)	C	1, 3
Balistidae					
Aluterus schoepfi				U	1, 4, 6
Aluterus scriptus				R	2, 7
Balistes capriscus				R	4
Balistes vetula				R	7
Canthidermis maculata				R	4
Monacanthus cilatus				C	1, 5, 10
Monacanthus hispidus				C	1, 5
Ostraciidae					
Lactophrys quadricornis				C	2, 4, 5
Lactophrys trigonus				U	1, 2
Tetraodontidae					
Chilomycterus antillarum				R	2
Chilomycterus schoepfi			C	C	1, 2, 4
Diodon histrix				R	1
Sphoeroides nephelus			C	C	1, 2, 4
Spoeroides spengleri			U	U	4, 5
Molidae					
Mola mola				R	7

* The citation codes are as follows: 1 = Tabb and Manning, 1961; 2 = Schmidt, 1979; 3 = Loftus and Kushlan, 1987; 4 = Roessler, 1970; 5 = Lindall et al., 1973; 6 = Thayer et al., 1987; 7 = Schmidt, 1975; 8 = G. Powell et al., 1987; 9 = Carter et al., 1973; 10 = Robins et al., 1991; 11 = Tabb et al., 1962; 12 = Tabb and Roessler, 1989; 13 = Clark, 1971; 14 = Henshall, 1891; 15 = Loftus, 1988; 16 = Robblee and Hutinet, unpub.; 17 = Jaanke, 1971; 18 = Trewavas, 1984; 19 = Collins and Finucane, 1984; 20 = Paulson, 1959; 21 = Loftus, personal obs.; 22 = UMML/EVER collections. PC = personal communication with the author, U = an unpublished work by the author.

TABLE 2. Fishes that may occur in Everglades National Park, but have not yet been collected there (Species of Hypothetical Occurrence). (I) = Introduced species.

Scientific name	Freshwater	Estuarine	Marine	Citation
Dorosoma cepedianum	X			Loftus and Kushlan, 1987
Echiophis intertinctus			X	Lindall et al., 1973
Menidia conchorum			X	Schmidt 1975
Syngnathus springeri			X	Carter et al., 1973
Hippocampus reidi			X	Carter et al., 1973
Centropomus ensiferus			X	Rivas, 1962
Serraniculus pumilio			X	Lindall et al., 1973
Serranus subligarius			X	Lindall et al., 1973
Astrapogon stellatus			X	Lindall et al., 1973
Diapterus auratus			X	Carter et al., 1973
Cynoscion nothus			X	UF collection
Chaetodon ocellatus			X	UF collection
Mugil gaimardianus			X	—
Lupinoblennius nicholsi			X	Carter et al., 1973
Hypleurochilus geminatus		X		Lindall et al., 1973
Chaenopsis ocellata			X	—
Gobionellus boleosoma			X	G. Tolley, 1983
Trichiurus lepturus			X	Carter et al., 1973
Sarda sarda			X	Carter et al., 1973
Bothus robinsi			X	Lindall et al., 1973
Syacium papillosum			X	Lindall et al., 1973
Esox americanus	X			Dineen, 1984; Trexler and Jordan, 1999
Pterygoplichthys multiradiatus (I)	X			Courtenay, 1997
Cichlasoma citrinellum (I)	X			Courtenay, 1997
Cichlasoma managuense (I)	X			Gestring and Shafland, 1997
Cichlasoma meeki (I)	X			Courtenay, 1997
Cichlasoma octofasciatum (I)	X			Courtenay, 1997
Geophagus surinamensis (I)	X			Courtenay, 1997
Hemichromis letourneauxi (I)	X			Courtenay, 1997

TABLE 3. The following species have been reported from the Everglades region, but there is no evidence to support their presence there. (Species of Doubtful Occurrence)

Scientific name	Freshwater	Marine	Citation
Lepisosteus osseus	X		Stevenson, 1976
Brevoortia tyrannus		X	Kushlan and Lodge, 1974
Notropis chalybaeus	X		Stevenson, 1976
Opsopoeodus emiliae	X		Stevenson, 1976
Anchoa cayorum		X	Schmidt, 1993
Aphrododerus sayanus	X		Briggs, 1958
Ophidion marginatum		X	Tabb and Roessler, 1989
Menidia menidia		X	Schmidt, 1975
Chaenopsis limbaughi		X	Thayer et al., 1987
Chasmodes bosquianus		X	G. Tolley, 1983
Sphoeroides parvus		X	Schmidt, 1993

ciliidae are numerically dominant (Loftus and Eklund, 1994; Trexler et al., 1996). The families Percidae, Cyprinidae and Catostomidae are represented in the park by only a few species. In the rest of North America, these families are predominant in most communities. The reasons for these differences probably include the absence of freshwater stream habitats and unfavorable abiotic conditions of heat, drought, and low dissolved-oxygen events.

Many fishes in the park inhabit more than one habitat. Peripheral freshwater species, which may survive in both fresh and salt waters, are numerous in park habitats (Loftus and Kushlan, 1987). Members of the speciose order Cyprinodontiformes may be found across the salinity gradient and are often very common where they occur. Other euryhaline fishes inhabit primarily marine and estuarine habitats, and occasionally move into fresh water. These number 83 species in the park, the majority belonging to three families of Perciformes: Haemulidae, Sciaenidae, and Gobiidae. Notably, Sciaenidae is the most diverse family in all park waters with 16 species.

There are 164 strictly marine fishes in the park. Of the Elasmobranchs, the requiem sharks (Carcharhinidae) are the most speciose. Seven families of Rajiformes are also present; however, no family is represented by more than three species. In the class Osteichthyes, the order Clupeiformes has two speciose families occurring within the park, Clupeidae and Engraulidae. The family Syngnathidae (order Gasterosteiformes) has numerous members in marine Park waters, as does the family Serranidae (order Perciformes). The jacks (Carangidae) are represented by 14 species, of which the crevalle jack (*Caranx hippos*) is especially common.

Although the body of research on freshwater fishes in Everglades National Park is small compared to work in marine and estuarine waters, the composition, abundance, and distribution of the freshwater fauna are better known. Marine and estuarine habitats are extensive and difficult to sample, so that the abundance and distribution of many species are poorly understood. However, some general characteristics of the saltwater fauna are obvious. The records show that most offshore pelagic species occur infrequently in the shallow park waters. The inshore marine fauna of southern Florida and the Florida Keys is very diverse, but many characteristic species are rare or absent in the park. Members of the inshore fauna are often associated with hard coral or worm reef habitats, which are mostly absent from park waters. Also, winter water temperatures are warmer on the ocean side of the Florida Keys than in park waters because of the moderating influence of the Florida Current. As a result, tropical reef species are uncommon in Everglades National Park and normally occur there only as strays.

Other habitat characteristics of Florida Bay and inshore areas of the Gulf of Mexico influence the composition of the fish community. Because estuarine habitats receive seasonally fluctuating amounts of freshwater runoff from the Everglades, salinities vary greatly during the year. The network of mudbanks restricts water circulation in Florida Bay, affecting biotic communities and resulting in ecological conditions different from those in contiguous marine habitats on either coast of the peninsula (Holmquist et al., 1989). Florida Bay may act as a barrier to gene flow for some fishes that have presumably disjunct ranges on the Atlantic and Gulf coasts.

Marine fishes exhibit seasonal movements related to spawning, immigrations to and from nursery grounds, and changes in temperature and salinity (Moe, 1972). Seasonal migrations include coastwise movements by species that spend either the summer or winter along the Florida coast, e.g., bluefish (*Pomatomus saltatrix*), mackerel (*Scomberomorus* spp.), and dolphin (*Coryphaena hippurus*), or may reflect localized movements by south Florida populations, e.g., spotted seatrout (*Cynoscion nebulosus*), and gray snapper (*Lutjanus griseus*). Many species as larvae or juveniles show ontogenetic movements into estuarine nursery habitats, then move offshore as they mature. Freshwater species in the Everglades exhibit limited movements among habitats related to changes in seasonal environmental conditions, especially the flooding or drying of the marshes (Loftus and Kushlan, 1987). Diadromous and euryhaline species, such as tarpon (*Megalops atlanticus*), American eel (*Anguilla rostrata*), and common snook (*Centropomus undecimalis*), commonly move between salt and freshwater habitats, spending time in both.

Nine introduced freshwater species have colonized the park during the past two decades, with seven species establishing breeding populations. The butterfly peacock bass (*Cichla ocellaris),* and the Mozambique tilapia (*Oreochromis mossambicus)* have not yet become established there. Several other introduced species are found in the canal system outside the park and may make their way into park waters in the future (Table 2). All non-native freshwater fishes in the park have their origins in the tropics or subtropics, and most were the result of aquarium or aquaculture introductions (Courtenay et al., 1974; Loftus, 1988; and Loftus and Kushlan, 1987). Most introduced species tolerate low to moderate salinities, so have colonized the mangrove region of the park. There are no exotic marine fishes known from the park.

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THE INFLUENCE OF SEAWALLS AND REVETMENTS ON THE PRESENCE OF SEAGRASS IN THE INDIAN RIVER LAGOON, A PRELIMINARY STUDY

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Abstract: *Various types of shoreline stabilization methods have been used in the Indian River Lagoon to prevent erosion caused by wave action. These include: vertical seawalls, smooth revetments, riprap revetments (all collectively referred to as hardened shorelines), and to a lesser extent, vegetated shorelines. It has been widely assumed that hardened shorelines are detrimental to the environment due to a scouring effect caused by backwash from wave action. The results of an extensive search of english-language literature indicate that (1) there is no published evidence linking hardened shorelines to a reduction in seagrass distribution or abundance, and, (2) in the conditions found in Indian River Lagoon, the theoretical scouring associated with vertical seawalls is limited to approximately 1–2 meters seaward from the wall for vertical seawalls, and considerably less for smooth and riprap revetments. Our field studies indicate that the presence of seagrasses adjacent to all types of shorelines, whether hardened or vegetated, is similar. The lack of seagrasses which typically occurs in the zone between 0–5 meters offhore must be due to some other factor or factors.*

The Indian River Lagoon, and other areas of the Intracoastal Waterway (ICWW) in Florida, contain many miles of natural and man-made shorelines subject to varying degrees of wave-induced erosion. In areas where erosion is perceived as a problem, various types of shoreline reinforcement methods have been constructed. These include: vertical seawalls, inclined seawalls (smooth or textured), rip-rap, and to a lesser extent, vegetated shorelines intended to provide wave attenuation. In 1991 the Florida Legislature, acting on the advice of several state agencies, passed legislation encouraging the use of vegetated shorelines, as opposed to the use of "hardened" shorelines. Florida Statutes 403.918(5)(a) states that "It is the intent of the Legislature to protect estuaries and lagoons from the damage created by construction of vertical seawalls and to encourage construction of environmentally desirable shore protection systems, such as riprap and gently sloping shorelines which are planted with suitable aquatic and wetland vegetation." Vertical seawalls are now generally prohibited, unless sloped rip-rap is placed along their seaward sides.

Recently, there has been much debate between state environmental agencies and environmental permit applicants regarding the use of inclined seawalls and rip-rap. The state agencies have taken the position that scouring caused by wave reflection from hardened shorelines extends 15 meters waterward from the toe of the structure (which is usually near Mean Water Level), and that hardened shorelines—particularly those associated with causeways—have resulted in adverse impacts to seagrasses. In order to obtain a permit to construct a hardened shoreline, permit applicants must provide mitigation for the presumed impacts to seagrasses. Usually mitigation consists of constructing or restoring some similar type of habitat within the same geographic area. Since mitigation ratios are typically about 2:1, and the state has estimated that mitigation costs average about $75,000/acre, it became important to know whether the assumed impacts could be validated in the scientific literature or in the field. This preliminary study, which addresses the impacts of hardened shorelines on seagrass distribution, is divided into two parts. The first part documents the findings of a literature review on (1) the presence and historic distribution of seagrasses in the Indian River Lagoon, with emphasis on seagrasses adjacent to hardened shorelines or causeways, and (2) the extent of scour, theoretical or measured, associated with various types of hardened shorelines. The second part presents the results of a limited field survey which measured the distribution and density of seagrasses adjacent to several types of hardened shorelines as compared to vegetated shorelines.

This report centers on seagrasses rather than other species, since seagrasses are the focus of state regulatory agency concerns, and are undergoing a long-term study effort as part of the Indian River Lagoon (IRL) restoration program conducted by the Indian River Lagoon National Estuary Program (IRLNEP), St. Johns River Water Management District (SJRWMD), the Surface Water Improvement and Management program (SWIM), the Marine Resources Council, and others. Seagrasses have been used as indicator species for studies on water quality and the impacts of human activities on estuarine ecology. Seagrass meadows have been described as the marine analog of tropical rainforests because of their structural complexity, biodiversity, and productivity (Simenstad, 1994), and the SWIM Plan has identified seagrass beds as "... the most critical habitat in the Lagoon," (Steward et al., 1994).

LITERATURE SEARCH—The first part of our literature search was intended to determine if there is any body of evidence linking hardened shorelines, or, as a sidenote, causeways in general, with a reduction in seagrass distribution and abundance. This was done using published reports, available public data on seagrasses in the IRL, and SJRWMD Geographical Information System (GIS) files that give snapshots of seagrass coverage in the IRL from 1943–1992.

Biology and ecology of seagrasses in the IRL—The first effort in the literature search was to summarize the requirements for seagrass growth, as they are currently understood. This was necessary in order to understand the normal limits of growth, so that any effects from scouring might not be mistaken for other growth-limiting factors.

The upper depth limits of seagrass occurrence are of primary concern to us, since hardened shorelines often terminate at the water's edge or in very shallow water. We, and the state environmental regulatory agencies, have assumed that any scouring effects would be manifested by limiting the upper extent of seagrass growth. That is, seagrass communities would be able to grow close to shore adjacent to vegetated shorelines, and would occur farther offshore adjacent to hardened shorelines. Unfortunately, we found no studies which addressed factors which may affect the upper limits of seagrass growth.

By contrast, there are numerous studies which discuss factors which affect the lower depth limits of seagrass growth. The primary determinant of the lower depth limits of seagrass is the penetration of photosynthetically active radiation (PAR—that part of the light spectrum usable by plants) through the water column (Duarte, 1991; Kenworthy and Haunert, 1991; Kenworthy, 1993; Goldsborough and Kemp, 1988; Stevenson et al., 1993; Dennison et al., 1993; Morris and Tomasko, 1993; Busby and Virnstein, 1993). Low PAR values caused by suspended solids, phytoplankton, epiphytic algae, and color can have a cumulative and chronic adverse impact on seagrass communities (Kirk, 1983). Decreased PAR availability within the IRL has been directly related to nutrification and sedimentation caused by stormwater runoff from the surrounding land use (Virnstein and Morris, 1996). In the IRL, a comparison of existing studies and historic aerial photographs covering approximately the last 50 years have estimated the lower depth limit of seagrasses in the IRL at 6 ft (Woodward Clyde Consultants, 1994). In situ data from monitoring transects in Hobe Sound, northern Indian River, southern Mosquito Lagoon, and northern Banana River (collected as part of the SJRWMD Submerged Aquatic Vegetation Initiative) have estimated the average maximum depth of seagrasses at 1.7m (5.5 ft) (Virnstein and Morris, 1996).

Distribution and abundance trends of seagrasses in the Indian River Lagoon—There has been a significant decline in seagrass distribution in the IRL during the past 50 years (Virnstein and Morris, 1996). The IRL-NEP report (Woodward-Clyde Consultants, 1994) summarized the types and sources of historical imagery, and analyzed them to describe the apparent status and trends of submerged aquatic vegetation (includes algae, but is mostly seagrass) distribution in the IRL system. The SJRWMD reanalyzed the imagery used in the IRLNEP report and converted the maps to GIS format. We obtained copies of these files and analyzed the data in the vicinity of Pineda Causeway (SR 404) and Merritt Island Causeway (SR 520) to determine any correlation between the reported decline in seagrass distribution and the construction of revetments, seawalls, causeways, or other artificial shorelines. Figures 1 and 2 show the earliest (1943)

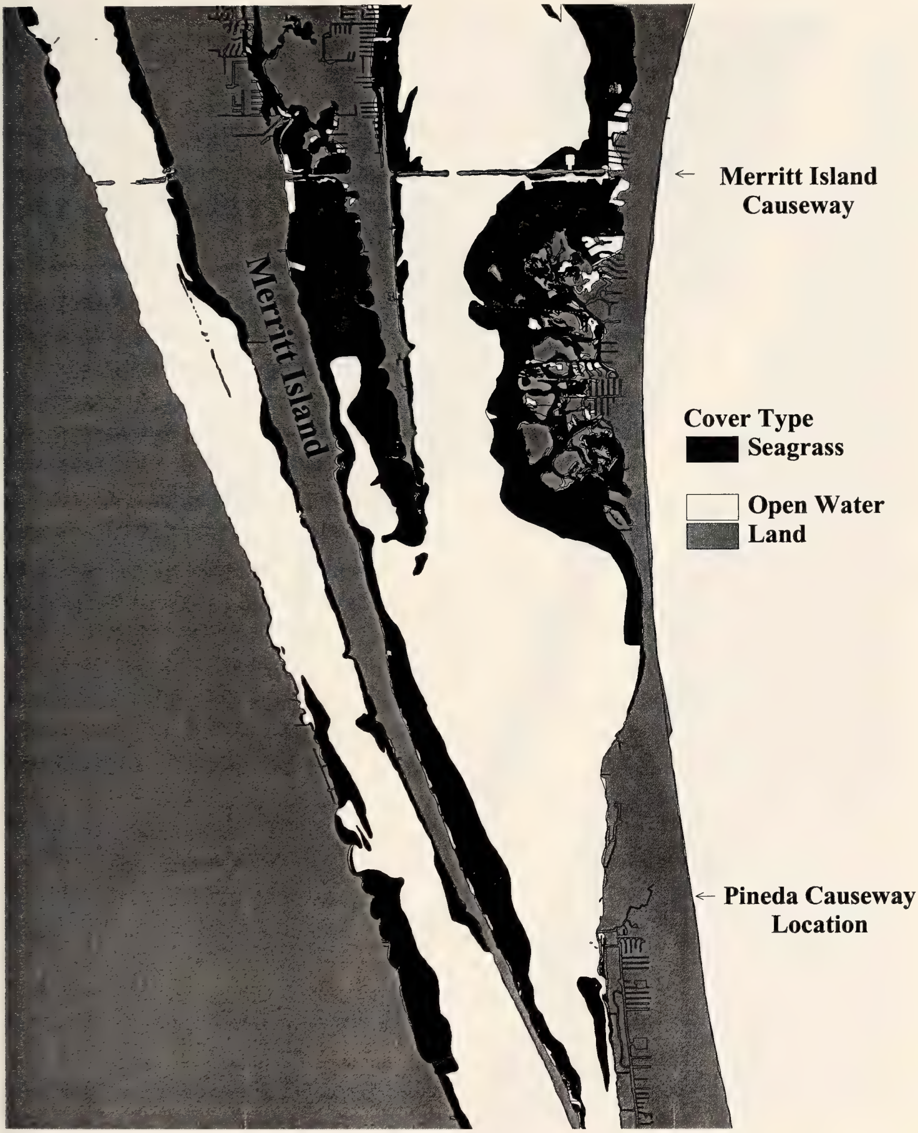

FIG. 1. 1943 seagrass coverage in the vicinity of Pineda and Merritt Island Causeways (source: SJRWMD GIS files).

and latest (1992) maps taken from the SJRWMD GIS files. From these maps, it can be seen that there has been a noticeable reduction in seagrass coverage since 1943. Most apparent is the loss along the east and west shores of the Indian River, and to a lesser extent, along the east shore of Merritt Island. According to SJRWMD (Virnstein and Morris, 1996), this loss is indicative of the area-wide decline due to water quality problems. Nothing in the GIS maps appears to implicate hardened shorelines along

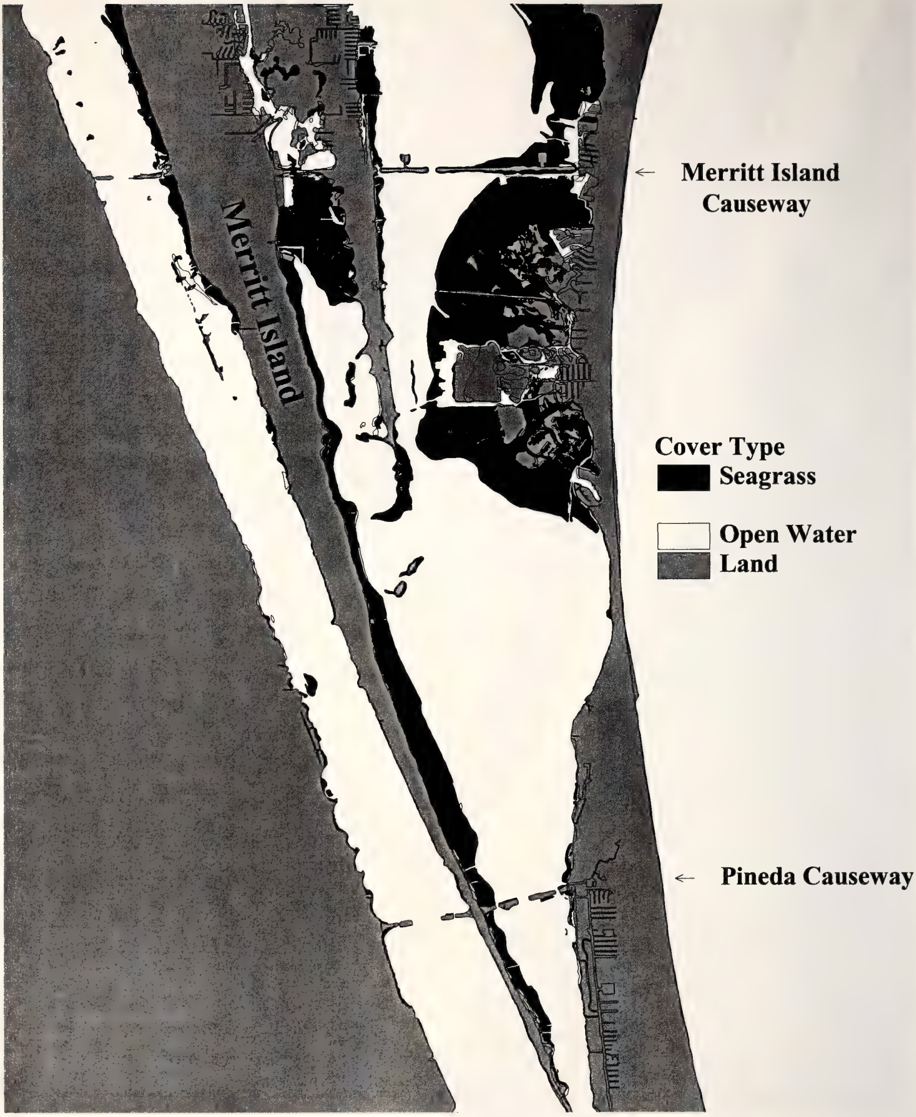

FIG. 2. 1992 seagrass coverage in the vicinity of Pineda and Merritt Island Causeways (source: SJRWMD GIS files).

the causeways as a significant factor in the loss of seagrass since 1943. At the same time, the maps show a small amount of seagrass recruitment along the sloped shelves of Pineda Causeway and Merritt Island Causeway, where depths were historically too great for seagrasses to become established. This observation is not intended to imply that causeway construction is beneficial to the environment.

Extent of scour associated with hardened shorelines—Scour refers to the movement of granular substrate (sand, in this study area) due to the hydrodynamic forces generated by waves and currents. It may occur rapidly or over a long period of time, and may be cyclic with infilling of the scour hole due to seasonal changes. For purposes of this study, it is assumed that any impacts to seagrass communities in the vicinity of hardened shorelines, as compared to vegetated shorelines, would primarily be due to wave induced scour. Scour due to flotsam (driftwood, trash), propellor scars, currents, and human use of the near-shore shallow waters appears to be insignificant, based on our field observations.

The engineering literature includes many references to beach stabilization efforts, but these are coastal and usually involve high-energy ocean waves. There are, however, a few references relating to shoreline stabilization and associated scour in shallow waters. Mathematical models for predicting scour associated with vertical seawalls have been developed by Xie (1985), and are considered to be reasonably accurate. Mathematical models for predicting scour caused by both smooth and porous (riprap) inclined seawalls have been developed and subsequently tested under laboratory conditions, but these are not considered to be reliable at this time (Kraus and McDougal, 1996).

Vertical seawalls are usually placed in deeper water, and scour can occur at the toes of such structures. The deeper the water, the less pronounced the scouring will be. The scour trough typically occurs at a distance of L/4 from the wall, where L is the wavelength of the incident wave (de Best et al., 1971). For natural conditions (irregular waves), most of the scour occurs within a distance of L from the seawall (Xie, 1981). This implies that in shallow estuarine areas with wavelengths during storm events on the order of 2 meters (as we have observed during several storm events in the IRL), the scour trough would be centered at approximately 0.5 meter from vertical seawalls, and scour influence would extend 1–2 meters outward. The scour depth is approximately equal to the nonbreaking wave height that can be supported by the water depth at the structure (Powell, 1987).

Inclined seawalls or revetments are generally located at the water's edge or in very shallow water. Under similar conditions, scouring at inclined seawalls or revetments is less than for vertical seawalls, and the lower the slope, the less the scouring (Herbich, 1990). Depth of scour also decreases greatly in inclined revetments having greater porosity, such as rubble riprap. Scour in inclined revetments is directly related to the height of wave run-up (R) on the structure, which in turn is related to the wave height (H). The energy absorption from rubble riprap results in run-up ratios, R/H, which are on the order of one third those for smooth structures (Silvester, 1990). Use of inclined rubble riprap structures should, therefore, result in the least amount of scour, compared to vertical seawalls or smooth-faced inclined revetments. No studies were found which addressed the relationship of scour to the use of planted vegetation alone or in combination with seawalls or revetments.

Distribution of Seagrasses at Hardened vs. Vegetated Shorelines—Most of the hardened shorelines we observed in the IRL terminate at the water's edge or in very shallow water (<0.3 meter below MWL). Any scouring impacts would occur from the edge of the hardened shoreline outward toward deeper water, with the greatest effects being closest to the shoreline. If scouring is a significant factor, then at vegetated shorelines where scouring is presumed to be minimal or absent, seagrasses should be able to grow closer to shore than at hardened shorelines. Therefore, our field studies focused on the upper limits of seagrass growth.

We located many suitable study areas along Pineda Causeway (State Road 404) and Merritt Island Causeway (State Road 520). Both causeways are located in Brevard County, Florida. Eau Gallie Causeway was also investigated, but since no seagrasses were found, it is not discussed in this study. The causeways were originally constructed of sand, and grass was installed on the slopes extending to the water's edge. From the water's edge, the bottom typically slopes gradually to a depth of about 2 meters at a distance of 50–100 meters offshore. Somewhat greater depths may occur farther offshore. Like much of the Indian River Lagoon, the area is essentially non-tidal. Although there is significant fetch when the wind blows from the north or south, the shallow depths in the lagoon result in relatively small wave heights and periods. During one storm event in 1996, we measured the average wave height at Pineda Causeway at approximately 0.6 meter. In spite of the small wave heights, the combination of storm winds and waves is sufficient to erode the causeways in places, and over the years a variety of shoreline stabilization methods have been used to repair the erosion. The causeways today include areas of vegetated shoreline (mangroves and grasses), riprap (limestone rocks), smooth inclined revetments, and vertical seawalls. Seagrasses have colonized the shallow littoral shelves of the causeways, and this provides an ideal scenario for the comparison of the effects of shoreline types on seagrass distribution.

Pineda Causeway and Merritt Island Causeway cross both the Banana and Indian Rivers, which are separated by Merritt Island (Figs. 1 and 2). The Indian River bottom contains more muck, while the Banana River bottom is primarily sand. As a result, the water in the Indian River tends to have relatively poor visibility, compared to the Banana River. The muck substrate and poor light penetration in the Indian River are less conducive to seagrass growth, as compared to the Banana River. Where seagrasses occur, *Halodule wrightii* is dominant, with lesser amounts of *Halophila englemanni.* Vegetated shorelines included in this study consisted primarily of mangroves (*Avicennia germinans and Laguncularia racemosa*) which typically occurred on the shoreline close to the water's edge. Inclined smooth revetments were constructed of interlocking blocks, which occasionally were vegetated in sparse patches with *Distichlis spicata.* Riprap revetments were constructed of rocks of approximately 0.5 meter diameter, and vertical seawalls were constructed of poured concrete.

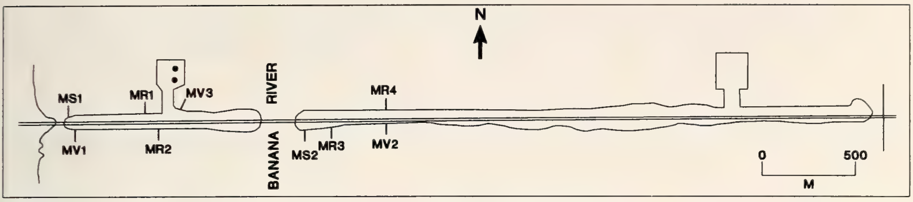

FIG. 3. Merritt Island Causeway transect locations (transect lengths shown enlarged for clarity).

Methods—In November and December, 1996, 9 transect stations were established along Merritt Island Causeway (Fig. 3), and in December and March, 1997, 15 transect stations were established along the Pineda Causeway (Fig. 4). Each transect was perpendicular to shore (within 10 degrees of north/south axis), and commenced at mean high water. Although this study is concerned with nearshore effects of seawalls and revetments, the transects were extended to 30 meters offshore, which is the approximate limit of the causeway littoral shelf. All transects appeared to have similar wave climates, particularly during storm events, but wave height measurements were not made as part of this study.

The transects were located using a Trimble Differential GPS unit with submeter accuracy, and the GPS data were downloaded into AutoCAD for plotting. The start and end points of seagrass beds along the transects were noted, and average density of the beds was determined by recording one meter square quadrats every 7 meters along the transects. At each quadrat, seagrass density was determined by a diver using methods described by Morris and Tomasko (1993). Seagrass data were not statistically evaluated to determine whether the transects represent the same population, since the focus of the study was on the lack of seagrasses in the nearshore areas. As a sidenote, the upper edges of the seagrass beds were clearly visible from shore on calm, sunny days.

Results—Tables 1 and 2 show the distance from shore and depth where seagrass beds started and ended (or exceeded 30 meters from shore). Table 1 presents data from Pineda Causeway, and Table 2 presents data from Merritt Island Causeway. The typical relationship between transects and distribution of seagrass beds is shown in Figure 5. Densities of seagrass communities ranged from sparsely vegetated (<10 percent) to moderately vegetated (10–40 percent cover), with occasional dense patches (40 percent or greater coverage). Since our study is intended to test the hypothesis that hardened shorelines may affect the upper limits of seagrass growth, using the above data, we determined the average distance from shore and depth

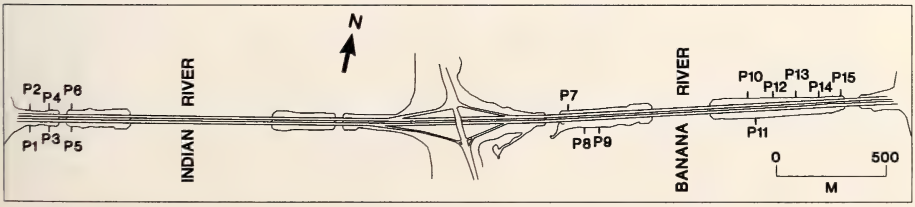

FIG. 4. Pineda Causeway transect locations (transect lengths shown enlarged for clarity).

TABLE 1. Distribution and density of seagrasses at Pineda Causeway.

Transects	Distance from shore (m) Start	End	Depth (m) Start	End	Substrate	Density[1]
Vegetated						
P1	7.0	26	0.3	0.9	Sand	M
P8	4.5	>30	0.3	1.5	Sand	M
P9	4.5	>30	0.3	1.0	Sand	M
P11	5.3	>30	0.2	1.0	Sand	M
Riprap Revetment						
P10	7.6	>30	0.5	1.7	Sand	S
P12	7.6	>30	0.6	1.9	Sand	M
P13	4.1	>30	0.4	1.3	Sand	S
P14	3.6	>30	0.3	1.6	Sand	S
Smooth Revetment						
P2	6.0	>30	0.2	1.1	Sand	M
P3	14	20	0.5	0.8	Rubble	S
P4	4.3	28	0.3	1.0	Sand	M
Vertical Seawall						
P5	7.6	22	0.6	0.9	Sand	S
P6	7.7	>30	0.4	>30	Sand	S
P7	7.6	>30	0.6	1.3	Sand	M
P15	8.0	>30	0.8	>30	Sand	S

[1] Density Codes: S = Sparse, M = Moderate, D = Dense.

at which seagrass communities commenced for each type of shoreline at each causeway.

Vegetated shorelines—At Pineda Causeway, seagrass beds commenced at an average of 5.3 meters offshore, in depths averaging 0.3 meter. At Merritt Island causeway, the values were 5.5 meters and 0.4 meter, respectively.

Riprap revetments—Seagrass beds at Pineda Causeway commenced at an average of 5.7 meters offshore and in 0.4 meter depth. Average values at Merritt Island Causeway were somewhat less, with seagrasses commencing at 3.8 meters offshore in 0.2 meter depth.

Smooth revetments—At Pineda Causeway, seagrasses commenced at an average of 8.3 meters offshore in depths averaging 0.3 meter. The average is increased because of one transect, P3, at which seagrasses did not appear until 14.7 meters offshore. The transect was included in the data set, although the substrate between 0–14 meters offshore consisted of rocky rubble and shell, and was considered by the investigators to be unsuitable for establishment of seagrasses. Eliminating this transect yields an average start

TABLE 2. Distribution and density of seagrasses at Merritt Island Causeway.

	Distance from shore (m)		Depth (m)			
Transects	Start	End	Start	End	Substrate	Density[1]
Vegetated						
MV1	6.0	7.6	0.5	0.8	Sand	S
MV2	6.0	>30	0.5	1.5	Sand	M
MV3	4.5	>30	0.2	1.0	Sand	M
Riprap Revetment						
MR1	3.9	>30	0.1	1.8	Sand	M
MR2	5.4	22	0.3	1.5	Sand	M
MR3	2.0	9.0	0.1	1.8	Sand	M
MR4	4.0	>30	0.2	1.5	Sand	D
Vertical Seawall						
MS1	3.0	>30	0.2	1.6	Sand	D
MS2	1.5	15	0.3	1.4	Sand	S

[1] Density Codes: S = Sparse, M = Moderate, D = Dense.

point of 5.1 meters offshore in 0.3 meter depth. There are no smooth revetments at Merritt Island Causeway, so comparative data between causeways are unavailable.

Vertical seawalls—Seagrasses at Pineda Causeway commenced at an average of 7.7 meters offshore in 0.6 meter depth. At Merritt Island Causeway, the values were 2.2 meters offshore and 0.3 meter depth. No scour troughs were observed at any seawalls.

The distance offshore and depths at which seagrass communities com-

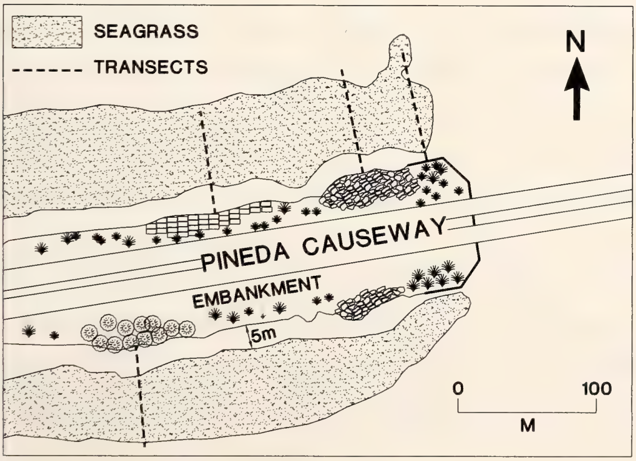

FIG. 5. Typical relationship between transects and seagrass beds.

TABLE 3. Upper limits of seagrass growth compared to shoreline type.

Shoreline type	Distance from shore, m (std. dev.)	Depth, m (std. dev.)
Vegetated	5.4 (0.90)	0.3 (0.12)
Riprap Revetment	4.8 (1.85)	0.5 (0.17)
Smooth Revetment[1]	5.1 (0.85)	0.3 (0.05)
Vertical Seawall	5.9 (2.62)	0.5 (0.20)

[1] Excludes transect P3 (unsuitable substrate).

menced are summarized by shoreline type in Table 3. Data from both causeways have been averaged, and standard deviation is reported. Paired t-tests and Mann-Whitney *U* tests were done by combining all data for each shoreline type, since it was not our intention to consider differences within individual causeways for this preliminary study. None of the tests indicated any significant differences at the 95% confidence level for vegetated shorelines as compared to any of the hardened shorelines. There is no indication that hardened shorelines within our study area inhibit the upper limits of seagrass occurrence, as compared to natural vegetated shorelines. Irrespective of shoreline type, the upper limit of seagrass growth appears to be about 5.3 meters offshore, and in 0.4 meter depth. It is noteworthy that out of 24 transects, only 3 had seagrasses growing closer than 4 meters from shore, and these 3 were adjacent to a vertical seawall and a riprap revetment.

The littoral shelf on both causeways typically extended about 30–40 meters offshore, and seagrasses did not extend beyond the shelf except in shallow areas near the natural shorelines. At Pineda Causeway, seagrass beds terminated at an average depth of 1.2 meters, and at Merritt Island Causeway, seagrass beds terminated at an average depth of 1.4 meters.

Within the seagrass beds, seagrass density appeared to be directly related to substrate suitability. Although the substrate is often reported as sand, there is usually an admixture of varying amounts of muck. The areas of lowest seagrass density had the highest muck content, and no seagrasses were found in areas where the substrate consisted entirely of muck. We made no attempt to determine the relationship between seagrass density and shoreline type, since substrate seemed to be the dominant factor. The majority of our transects consisted of moderate seagrass growth, regardless of shoreline type.

CONCLUSIONS—Although over 2,500 published literature references were investigated, no specific references regarding effects of hardened shorelines on seagrass distribution and abundance for any geographic area were found. For the Indian River Lagoon, the consensus of the reviewed literature was that a reduction in water clarity caused by nutrification and sedimentation, and a reduction in the available shallow-water habitat (due to dredging and filling) were the main causes of seagrass loss over the past 50 years. The available GIS data do not support the hypothesis that hardened shorelines have been a significant factor in the lagoon-wide seagrass loss. Although construction of the causeways likely resulted in placement of fill on seagrass habitat, seagrasses have increased within the vicinity of the causeways due to colonization of the causeway slopes where post-construction depths were more conducive to their growth.

The engineering literature was in agreement that vertical seawalls had the greatest potential for scour, followed by smooth revetments, then riprap revetments. However, in shallow inland waters, the degree of scour for any type of hardened shoreline is calculated to be small. For vertical seawalls (the worst case) in shallow water, the scour trough occurs at a distance of L/4 from the wall (L = wave length). During the period of our studies, which included several storm events, we estimated wave heights at 0.6 meters, and wave lengths at 2.2 meters. Therefore, any scour trough formed should be 0.6 meter from the seawalls. Taking wave heights into account, even with strong storms, the influence of scour should not extend more than 1–2 meters offshore at vertical seawalls, perhaps half that for a smooth revetment, and a fraction of a meter for a riprap revetment (depending on the size of riprap rubble). Since no scour troughs were observed at any hardened shoreline, it may be that recent storm events have not been of sufficient duration for scour troughs to develop, or perhaps they refill relatively quickly in calm weather conditions.

The results of our preliminary field studies support our findings in the scientific and engineering literature. Considering all vegetated shorelines, seagrass beds commenced at an average of 5.3 meters offshore. Averaging vertical seawalls and riprap revetments at both causeways results in values of 5.9 meters and 4.8 meters, respectively. Averaging all types of hardened shorelines, seagrasses commenced at 5.5 meters offshore. With few exceptions, seagrass beds extended to a depth of approximately 1.5 meter, which was either at the edge of the littoral shelf, or >30 meters. Density levels were similar for all shoreline types.

It is hoped that additional transect data can be collected in the future, so that in-depth statistical analyses can be done. In the meantime, what stands out from this preliminary study is the fact that there was no major difference in distance offshore at which seagrass beds commenced among any of the hardened shoreline types as compared to vegetated shorelines.

The presumption by state agencies that the scour zone associated with hardened shorelines extends to approximately 15 meters offshore, and that there would be a loss of seagrass communities within that zone, is not supported by published literature or the present field study. The conclusions from this literature search and field study are: (1) the scour zones at all types of hardened shorelines in shallow waters is very small, perhaps on the order of 0.5–2.0 meters, and (2) hardened shorelines in shallow estuarine waters appear to have no major effect on seagrass distribution or density, as compared to vegetated shorelines.

The question of why the seagrasses do not generally occur within the first 5.3 meters from shore remains to be answered. Based on our direct observations, we offer two possible explanations: (1) During windy conditions, we observed that the waves generally break around 5 meters offshore. Breaking waves create relatively high turbulence levels in the shallow depths, most of which consist of sandy substrate. Although scour from shore features is absent, the wave-generated turbulence in shallow depths may be sufficient to prevent seagrasses from taking hold. Recalling that wave heights of 0.6 meter were observed, and that waves break in depths approximately equal to 2/3 the wave height, this could explain why the upper limit of seagrasses adjacent to all shorelines occurs at about 0.4 meter depth. (2) We observed that filamentous algae, including epiphytic types, are far more profuse in the shallow waters close to shore. In fact, seagrass at the upper edge of the beds had so much epiphytic algae that it appeared to be dying and decaying. Other researchers have noted that epiphytic algae can affect the growth and survival of seagrass (Busby and Virnstein, 1993). It may be that the warmer shallow water, with greater amounts of light, allows the filamentous algae to out-compete the seagrass. If either hypothesis is true, the type of shoreline stabilization within our study area would be essentially insignificant to the distribution of seagrass. Future research should include wave recorder data to quantify wave action at various depths and distances from shore, as well as detailed studies on the effects of epiphytic algae on seagrass at various depths, especially in shallow waters.

ACKNOWLEDGMENTS—We wish to thank Kristie Kaub and Mike Werle (EMS) for GIS and AutoCAD assistance, Lori Morris and Bob Day (St. Johns River Water Management District) for background information and literature sources, and Tianjia Tang (FDOT) for peer review. This project was supported in part by Florida Department of Transportation, District V, and St. Johns River Water Management District.

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REVIEW

Stevie Daniels (editor), *Easy Lawns: Low Maintenance Native Grasses for Gardeners Everywhere,* Brooklyn Botanic Garden, 21st-Century Gardening Series, Brooklyn, NY. 1999. Pp. 112. Price: $9.95.

AT first glance, this handy little volume appears to be one more of a long line of humdrum gardening handbooks, until the eye is caught by the word "native" in the subtitle. This, we see, is not to be a rehash of conventional wisdom (or foolishness) about keeping grass happy with an endless cycle of mowing, spraying, watering and weeding. It is in fact a book worth the attention of environmentalists as well as any homeowner yearning for freedom from the weekly lawn ritual.

This book really is about native plants, specifically grasses and other low-growing plants that can be used to create an attractive green lawn without all the work, polluting chemicals or aquifer-depleting sprinkling. It's arranged by region, so after the introductory section on how to establish a lawn, we can skip forward to the section on Native Lawns for Florida, contributed by our own Craig Huegel. We find that, although perhaps not suitable for making golf greens, a number of native grasses will provide an attractive, carefree ground cover. These include wire-grass, the low panicums, basket grass and several others. The growth form and cultural requirements for each species are clearly described. There's even a listing of nurseries where these often hard-to-find grasses can be obtained. Another attractive idea featured in the book is to add low-growing wildflowers that can come up amongst the grass clumps, often in early spring before the grass begins growing.

This well-written, informative and inexpensive book is a must for anyone, anywhere in North America, who is planning a new or replacement lawn.—Frederick B. Essig, Department of Biology, University of South Florida, Tampa, FL 33620.

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CONTENTS

Ages of Two Speleothems from Florida Caverns by U-Series Dating Methods .... J. K. Osmond and Adel A. Dabous 65

Evaporation and the Precipitation-Evaporation Balance in Florida Bay .... Ned P. Smith 72

The Herpetofauna of Everglades National Park .... Walter E. Meshaka, Jr., William F. Loftus, and Todd Steiner 84

A New Record for *Schistocerca ceratiola* (Orthoptera: Acrididae) ...... Jason M. Squitier 104

A Comparison of Scrub Herpetofauna on Two Central Florida Sand Ridges .... Lyn C. Branch and D. Grant Hokit 108

Use of a Computer-Interfaced System for Determination of the Inhibition of Oxygen Production by Selected Aquatic Weeds in the Presence of Cattail (*Typha domingensis*) Extracts .... Dawn M. Ambrogio, Maria T. Gallardo, Robert F. Benson, and Dean F. Martin 118

Isotope Analysis of Galena from Prehistoric Archaeological Sites in South Florida Robert J. Austin, Ronald M. Farquhar, and Karen J. Walker 123

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Geological Sciences

AGES OF TWO SPELEOTHEMS FROM FLORIDA CAVERNS BY U-SERIES DATING METHODS

J. K. OSMOND AND ADEL A. DABOUS

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ABSTRACT: *Two stalagmites from the Florida Caverns at Marianna were dated using uranium series methods ($^{230}Th/^{234}U$). Both grew rapidly, one 73,000 ± 5,000 years ago, and the other 53,000 ± 7,000 years ago. The ground waters from which they precipitated carried U with different $^{234}U/^{238}U$ activity ratios, and the two exhibited different initial $^{230}Th/^{232}Th$ contamination ratios, as revealed by the isochron method of age correction. The times of growth of the Florida Cavern speleothems do not appear to have been governed by glacial and climatic cycles as is the case for those in higher latitudes.*

THE Florida Caverns, near Marianna in Northwest Florida (Fig. 1), occur in the Crystal River Formation of the Ocala Group limestone of Late Eocene age. It is the only dry, exposed cave system in the state (Schmidt, 1988). The cave is a feature of the Marianna Lowlands karst region, which has been exposed to surficial weathering and erosion for much of post-Eocene time. A lower limit for the age of the cave itself would be the age of the speleothems that are a principal attraction for visitors.

Speleothems in limestone terrains usually form as a result of the solution and reprecipitation of calcium carbonate ($CaCO_3$) by infiltrating rain waters charged with CO_2 from the soil horizon (Hendy, 1971). The reprecipitation of calcite results in the incorporation of U (^{238}U and ^{234}U) but not of the daughter ^{230}Th, which is immobile in ground waters. Subsequent ingrowth of the thorium daughter (half-life = 75,000 years) is the basis for U-series dating. The necessary conditions are: (1) sufficient U for accurate measurement, (2) a minimum of occluded detrital impurities, (3) a closed, unrecrystallized system, and (4) an age less than 350,000 years.

Because they all decay by alpha emission, these U and Th isotopes can

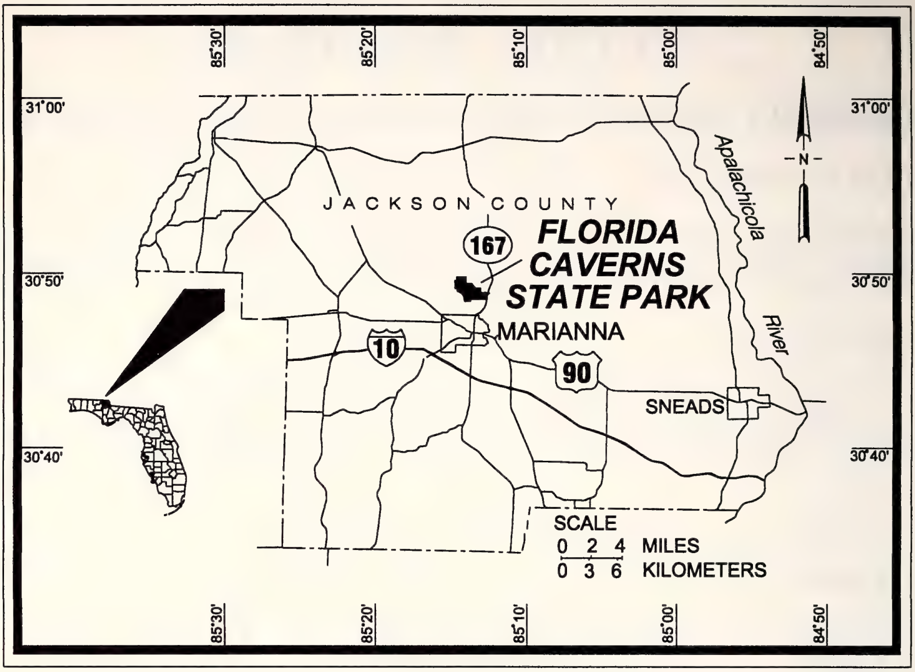

FIG. 1. Location map of Florida Caverns.

be measured accurately by alpha spectrometers of the type available at the Isotope Geochemistry Laboratory at Florida State University in Tallahassee.

METHODS—The two speleothems analyzed were obtained from the Department of Geological Sciences at Florida State University (specimen A) and from the Florida Geological Survey (specimen B). The exact locations within the cavern are unknown. Each specimen, 8–10 centimeters in diameter, was sectioned and sampled from concentric growth bands, labeled outer (1), middle (2), and inner (3).

Samples weighing from 20 to 40 grams were dissolved in nitric acid and isotopic yield tracers added, as described by Luo and Ku (1991). An equilibrated ^{232}Th/^{228}Th spike was used for specimen A and isotopes ^{236}U and ^{229}Th were added as tracers for specimen B. The samples were analyzed by alpha spectrometry using methods described by Lally (1992) and Ivanovich and Murray (1992).

The basic dating equation is:

$$^{230}\mathrm{Th}/^{234}\mathrm{U} = 1 - \exp(-0.692(t/T)) \qquad (1)$$

which describes the growth toward equilibrium of daughter thorium in a system with original U only, where t is the age of the system and T is the half-life of ^{230}Th, approximately 75,000 years.

However, there are two corrections which must be applied to the basic equation in order to obtain a true age. First, the ^{234}U is itself an intermediate daughter of the ^{238}U decay chain, and is often out of equilibrium in natural waters. The parameter ^{234}U/^{238}U changes with time as governed by the ^{234}U half-life, approximately 250,000 years. Inasmuch as both ^{230}Th and ^{234}U are changing with time, an iterative calculation procedure must be used to solve for t. We used

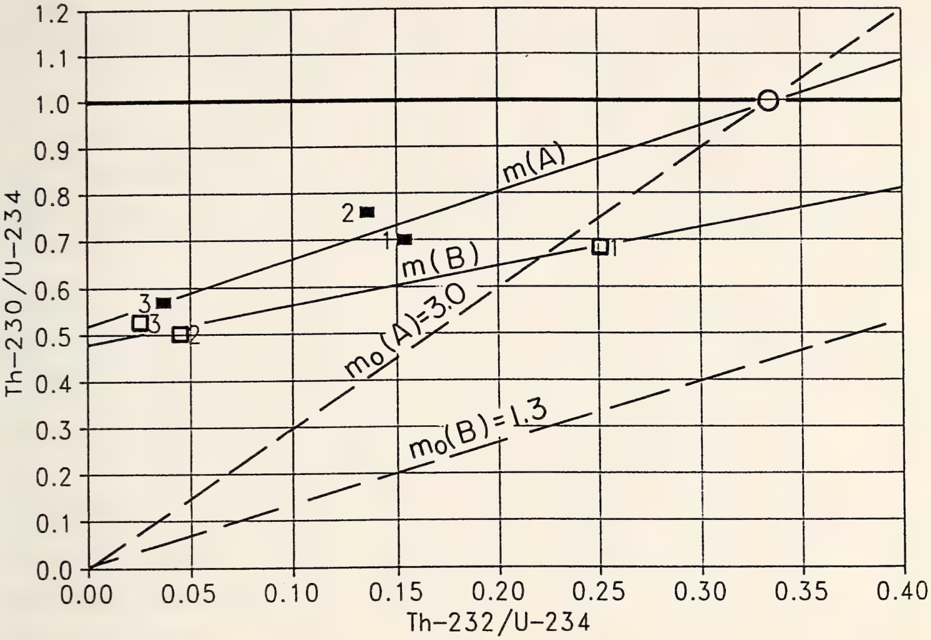

FIG. 2. Thorium correction isochrons for stalagmites A (solid squares) and B (open squares) from Marianna Caverns. Stalagmite A experienced an initial ^{230}Th/^{232}Th contamination ratio of 3.0 (dashed line) and has a corrected ^{230}Th/^{234}U dating ratio of 0.52 (solid line). Stalagmite B had an initial contamination ratio of 1.3 (dashed line) and has a corrected dating ratio of 0.48 (solid line). The solid and dashed lines show how the initial contamination ratio for the stalagmites was determined: by the intersection of the best-fit sample line (solid) with the equilibrium line at ^{230}Th/^{234}U = 1.0 (open circle)(see text). The two stalagmites also differ in their U content and in their ^{234}U/^{238}U activity ratios.

the program of Ludwig and Titterington (1994) to arrive at "apparent ages" of the individual samples. Secondly, these ages also need correction, to take into account the presence of initial ^{230}Th which occurs in the form of small amounts of detrital or colloidal material incorporated into the carbonate at the time of deposition.

The usual way to make this initial ^{230}Th correction is to measure the common thorium (^{232}Th) in the carbonate and assume that it is accompanied by some proportional amount of ^{230}Th. One possibility for this ^{230}Th/^{232}Th activity ratio would be a value in the range 0.43–1.12, typical of detritus (Gascoyne, 1992); another might be 1.7, as recommended by Kaufmann (1993) based on a survey of published data. We did not use this approach for two reasons: a) any estimate for the correct ratio at Marianna Caverns would be speculative, and b) an objective method for obtaining this ratio is available if the speleothems grew rapidly, on a 10^3 year time scale.

The apparent ages (corrected for ^{234}U excesses only) lead to inconsistencies, in which outer samples appear to be older than inner, which are best explained if each stalagmite's outer and inner layers are approximately the same age; and the variations in dating ratio are attributed to initial contamination with common thorium. Using non-radiogenic thorium as normative, the best fit line on the ^{230}Th/^{234}U vs. ^{232}Th/^{234}U plot defines an "isochron" (Fig. 2), whose slope varies as a function of age. The intersection of this line with the equilibrium line (^{230}Th/^{234}U = 1.0) defines the original contamination ratio. The y-axis intercept of the isochron line corresponds to the true, uncontaminated age of the sample suite. This method of correcting for initial thorium was developed by Osmond and co-workers (1970) to date beach rock formations at Cape Canaveral, Florida; its statistical validity has been addressed by Bischoff and Fitzpatrick (1991), and by Kaufman (1993).

RESULTS—The results of the U and Th isotopic analyses of the two stalagmites from Marianna Caverns are given in Table 1, which lists the "apparent age" of each sample analyzed, and also the isochron age for each stalagmite. The graphs on which the isochrons were constructed are shown in Fig. 2.

The apparent ages for each sample (outer, middle, and inner) for each of the two stalagmites (A and B) are based on the iterative calculation using measured ^{230}Th/^{234}U and ^{234}U/^{238}U activity ratios. But these apparent ages are misleading in that they are not corrected for initial contaminating ^{230}Th. In fact, in both stalagmites the inner sample appears to be younger than the outer, a relationship inconsistent with peripheral growth.

This anomaly disappears if the assumption is made that each stalagmite grew fairly rapidly, over a time span of a few thousand years. This is consistent with growth rates for a Holocene speleothem in a variable climate as calibrated by radiocarbon dating by Railsback and co-workers (1994). The specimens when sectioned gave no indication of the presence of growth hiatuses, such as marked color discontinuities. The apparent age differences, we conclude, can be explained by variations in the amounts of contaminating thorium. The data from each of the two stalagmites define a different correction isochron (see procedures, above), yielding different detrital thorium activity ratios and different ages. Stalagmite A formed 73,000 ± 5,000 years ago and incorporated varying amounts of contaminating thorium, having a ^{230}Th/^{232}Th ratio of 3.0, the greatest amount entering during the middle and outer stages of its growth. Stalagmite B formed 53,000 ± 7,000 years ago, incorporating thorium with a ^{230}Th/^{232}Th ratio of 1.3, and it also suffered the greatest contamination during its final stage of growth.

The solutions which formed these two speleothems also differed in their uranium content. Ground waters forming stalagmite A contained uranium with a ^{234}U/^{238}U activity ratio of 1.04–1.08, while B waters had an activity ratio of 1.19–1.41. Stalagmite A contains, on average, about half the concentration of uranium as stalagmite B.

DISCUSSION—An advantage of the isochron method of correction for initial ^{230}Th is that the ambient ^{230}Th/^{232}Th activity ratio is revealed by the trend line itself, provided only that the samples defining the line are coeval. That this ratio exceeded the normal detrital ratio of 0.8 (Lin et al., 1996) suggests that a hydrogenous component may be involved. Such Th would have been carried by the ground water either as a dissolved or colloidal component, and it would not be surprising if the two speleothem sites at Marianna Caverns were to exhibit different ratios.

Published surveys of speleothem and travertine dating could be inter-

TABLE 1. Isotope data and apparent and corrected ages for two Marianna speleothems.

	Concentrations		Activity Ratios			
Sample	U (ppm)	Th (ppm)	$^{234}U/^{238}U$	$^{232}Th/^{234}U$	$^{230}Th/^{234}U$	Ages (ka)
Stalagmite A						
1 Outer	0.35 ± 0.01	0.168 ± 0.006	1.04 ± 0.02	0.154 ± 0.008	0.70 ± 0.02	120 ± 8
2 Middle	0.18 ± 0.01	0.074 ± 0.003	1.04 ± 0.02	0.136 ± 0.007	0.76 ± 0.02	141 ± 11
3 Inner	0.15 ± 0.01	0.018 ± 0.002	1.08 ± 0.03	0.037 ± 0.004	0.57 ± 0.02	81 ± 6
	Corrected $^{230}Th/^{234}U$ activity ratio (Fig. 2)				0.52 ± 0.02	
	Corrected age for Stalagmite A					73 ± 5
Stalagmite B						
1 Outer	0.032 ± 0.02	0.128 ± 0.013	1.41 ± 0.11	0.251 ± 0.042	0.68 ± 0.05	69 ± 11
2 Middle	0.27 ± 0.01	0.018 ± 0.002	1.27 ± 0.09	0.045 ± 0.004	0.51 ± 0.02	55 ± 6
3 Inner	0.30 ± 0.01	0.011 ± 0.001	1.19 ± 0.06	0.026 ± 0.002	0.53 ± 0.02	63 ± 6
	Corrected $^{230}Th/^{234}U$ activity ratio (Fig. 2)				0.48 ± 0.02	
	Corrected age for Stalagmite B					53 ± 7

preted as showing that the most common times of growth were during odd-numbered oxygen isotope climatic stages, corresponding to interglacials (Hennig et al., 1983; Schwarcz, 1986). However, most of the sites reviewed are from high latitude areas, where higher temperatures during interglacial times stimulated vegetation growth and increased soil carbon dioxide levels. Speleothem growth ceased or slowed during glacial intervals.

However, the climatic fluctuations in Florida were less extreme, and it remained relatively warm and moist during glacial intervals. There is less reason to expect that speleothem growth at Marianna would be governed by the advance and retreat of distant glaciers. According to the oxygen isotope time scale of Martinson and co-workers (1987), the 73 ka stalagmite grew at the very end of glacial stage 4 and the 53 ka stalagmite grew during the height of interstadial stage 3.

Both stalagmites grew rapidly and ceased growth after only a few years. Both record periods of greater detrital contamination during their later stages of growth. Ground water circulation must have changed between the two growth episodes, given the distinctly different uranium isotopic signatures of the two speleothems.

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EVAPORATION AND THE PRECIPITATION-EVAPORATION BALANCE IN FLORIDA BAY

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ABSTRACT: *Weather and water temperature data from two study sites in the northern part of Florida Bay are used to describe freshwater gains and losses by precipitation and evaporation from December 1996 to March 1997. Weather data from a third study site in southern Florida Bay provide estimates of evaporative water losses from July to December 1998, and from February to July 1999. Average evaporation rates at Johnson Key and Butternut Key in northern Florida bay are 0.015 and 0.012 cm* h^{-1}*, respectively. High-frequency fluctuations about the mean are irregular, and a consistent diurnal cycle is poorly defined. Day-to-day maximum evaporation rates are highly variable, with evaporative losses usually exceeding 0.02 cm* h^{-1} *and occasionally exceeding 0.06 cm* h^{-1}*. At both Johnson Key and Butternut Key, freshwater gains during the winter dry season are substantially less than evaporative losses. Results from southern Florida Bay include an average evaporative loss of 0.024 cm* h^{-1} *during the first of two field studies, and 0.023 cm* h^{-1} *during the second. Again, high-frequency variability is prominent, and the diurnal cycle is poorly defined.*

FLORIDA Bay lies at the southern end of the Florida Peninsula (Fig. 1). It is bounded on the north by the Everglades, and on the east and south by the Florida Keys. The western side of the bay is not defined by topographic features, and the 81°05′W meridian is often used to define the open western boundary. The surface area of the bay east of 81°05′W is approximately 2220 km^2. Water depths in the interior of the bay are generally 1–2 m, however extensive mud banks with depths less than 1 m are found in the northern and eastern parts of the bay. Mud banks and mangrove islands partition the bay into a series of sub-basins. Relatively narrow connecting channels inhibit the movement of water through the interior of the bay. Residence times have not been determined, but tidal and wind-forced exchanges are small in the northern and northeastern parts of the bay. Depths in the southern part of the bay are generally 2–3 m. Results from a series of circulation studies suggest a net west-to-east transport through southern Florida Bay (N. Smith, 1994, 1998; Wang, 1998).

The hydrology of Florida Bay is poorly understood, in spite of its fundamental importance to the ecology of the bay. Because of restricted circulation, local freshwater gains and losses are important factors in controlling salinity. Climatological data (NOAA, 1987) suggest that the average

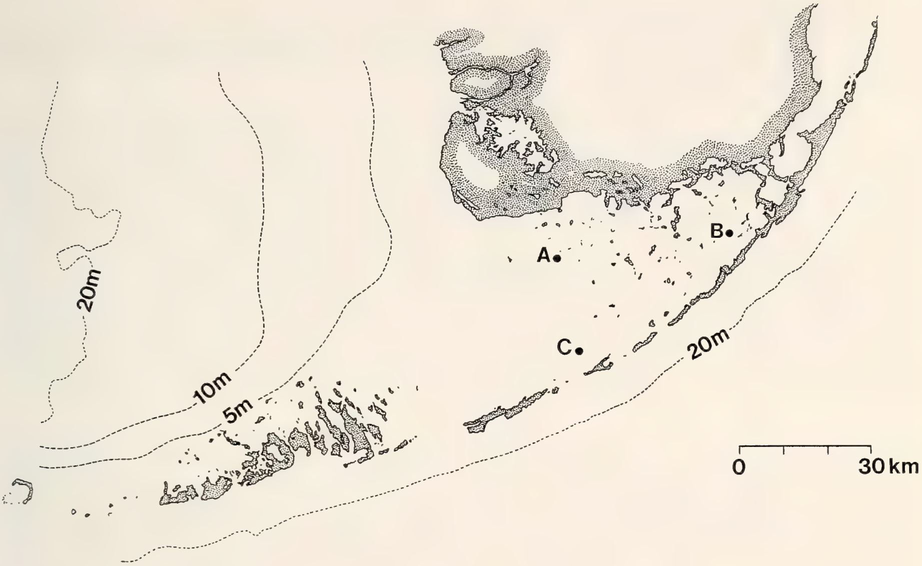

FIG. 1. Map of Florida Bay showing locations of weather stations at (A) Johnson Key and (B) Butternut Key in northern Florida Bay, and the Coastal-Meteorological Automated Network platform (C) in southern Florida Bay.

annual rainfall should be between 146 cm (Miami) and 100 cm (Key West), although rainfall totals in wet and dry years may differ significantly from the mean. Unpublished data from the National Park Service Marine Monitoring Network (D. Smith, 1998) indicate a mean annual rainfall of 126 cm at the southern tip of the Florida Peninsula, with totals ranging from 106 to 137 cm during 1993 to 1997. Approximately one-fourth of the total precipitation falls during the dry season months of November–April, and three-fourths of the total falls during the May–October wet season. Evaporative water losses have not been estimated for Florida Bay, and groundwater entering the bay from the Florida Peninsula has not been quantified.

During a 13-month period starting in March 1996, the Army Corps of Engineers Waterways Experiment Station (WES) conducted a field study in Florida Bay that included weather stations at Johnson Key and Butternut Key ("A" and "B" in Fig. 1). Surface water temperature was not recorded, but data from the National Park Service Marine Monitoring Network collected during the WES study complement the weather data and permit estimates of evaporative water losses from the bay. Rainfall measurements during the same time period can be combined with evaporation calculations to quantify the precipitation-evaporation balance. Since late 1992, weather data have been recorded in southern Florida Bay at a National Data Buoy Center Coastal-Meteorological Automated Network (C-MAN) weather station ("C" in Fig. 1). C-MAN data do not include any measure of atmospheric moisture, but a relative humidity sensor was attached to the tower starting in mid summer 1998, thereby permitting calculations of evaporative water losses. Rainfall is not recorded, and precipitation-evaporation balances cannot be determined at this location.

The purpose of this paper is to characterize freshwater gains and losses over time scales on the order of hours to weeks. Because of the short length of individual field studies, and due to significant seasonal and interannual variability in weather, estimates of evaporative losses over seasonal and annual time scales are tentative. The combination of meteorological and hydrographic data permit calculations of evaporation at all three stations, and of the precipitation-evaporation balance at the two study sites in the northern part of the bay. Results provide information on hydrologic processes that control the salinity, especially in the poorly flushed interior of Florida Bay.

DATA COLLECTION—WES weather stations were installed on platforms over open water. Weather and surface water temperature data at Johnson Key were available during an 84-day time period from December 10 1996 to March 5 1997. Weather and water temperature data were available from Butternut Key during a 104-day time period from December 6 1996 to March 20 1997. The WES weather stations recorded air temperature, relative humidity, atmospheric pressure and wind speed and direction. The accuracy of the air temperature readings is ±0.4°C according to instrument specifications, and the accuracy of the relative humidity against field references is ±2%, with a long-term drift of less than 1% per year. Humidity was checked at Johnson Key and Butternut Key in mid March 1997 using a sling psychrometer, and errors were assumed to accumulate linearly during the study. The accuracy of wind speed readings is 1 m s^{-1}, according to instrument specifications.

The C-MAN weather station recorded air pressure with an accuracy of ±1.0 hP, air temperature and water temperature with an accuracy of ±1.0°C and wind speed with an accuracy of ±1.0 m s^{-1}. A Telog R2126 temperature and relative humidity sensor was installed on the C-MAN tower to complete the data base needed to estimate evaporative water losses, and measurements were made hourly over a 135-day time period from July 28 to December 11, 1998, and over the 156-day period from February 3 to July 9, 1999. Relative humidity readings have an accuracy of ±3% according to instrument specifications. Calibration data taken with a sling psychrometer before, during and following the first study indicated errors of −3.4, +4.7, +1.1 and −0.9%. Data obtained before, during and following the second study indicated errors of −3.3, +2.8, 0.0 and +1.8%.

C-MAN water temperatures are recorded approximately 1 m below the surface. To investigate near-surface temperature gradients during times of light winds and strong insolation, an Onset Computer Corporation StowAway TidbiT temperature logger was attached to the bottom of a plastic foam float. Temperatures were recorded hourly approximately 5 cm below the surface and with an accuracy of ±0.2°C.

METHODS—Evaporative water losses were estimated with the bulk aerodynamic formula suggested by Pond and co-workers (1974):

$$E = \rho_a C_E V \Delta q, \tag{1}$$

where ρ_a is the density of the air in g cm^{-3}, C_E is a nondimensional bulk aerodynamic coefficient (the Dalton Number) that varied as a function of wind speed and stability in the lowest few meters of the atmosphere (Smith, 1988), V is the scalar average wind speed in cm s^{-1} and Δq is the specific humidity difference between the water surface and the level at which the weather observations are recorded. Air density was calculated as a function of air pressure and virtual temperature (List, 1963). Scalar average wind speeds measured 7 m above the water surface at the C-MAN station and 5.2 m above the surface at Johnson Key and Butternut Key were adjusted to approximate 10-meter level readings by assuming a power-law profile:

$$V_{10} = \left(\frac{10}{Z}\right)^{0.1} V_Z, \tag{2}$$

where V_Z is the wind speed measured at height Z above the water surface. With an exponent of 0.1 (Kourafalou and co-workers, 1996), 5.2 m level winds are multiplied by 1.068 to estimate 10 m level winds, and a 1.036 correction is applied to the 7 m level winds. These corrections are nearly identical to those obtained by assuming a logarithmic profile with a dynamic roughness of 0.025 cm (Brocks, 1962).

Hourly evaporation rates are plotted as a function of time to emphasize short-term variability, although lower-frequency fluctuations over time scales on the order of several days are also apparent in the plots. For ecological applications, the precipitation-evaporation difference (P − E) is of primary concern, because it is the net gain or loss of water that will lower or raise salinity. Rainfall data from the two weather stations in northern Florida Bay are combined with evaporation estimates and presented as cumulative net water gain. Plots of P-E are conceptually similar to water level time series obtained from evaporation pan measurements uncorrected for rainfall.

Diurnal variations in evaporative water loss are characterized using a Buys-Ballots averaging technique that averages all the 0100, 0200, etc. evaporation rates from a given time series. This obscures day-to-day differences in the diurnal cycle by constructing a mean diurnal variation. Buys-Ballots averaging is helpful also for characterizing diurnal cycles in wind speed and humidity gradients. Autocorrelation coefficients (Panofsky and Brier, 1958) are calculated to examine the diurnal cycle and determine if highest and lowest evaporative water losses are consistent in magnitude and in the time of day at which they occur.

The sensitivity of evaporative water loss estimates to variations in humidity, wind speed and air and water temperature was examined by raising or lowering measured values and recalculating evaporation. Variables were increased or decreased by an amount equal to the accuracy of the sensors. For example, when humidities were raised and lowered by 3%, evaporative water losses decreased and increased by 11%, respectively. Sensitivity to wind speed was somewhat larger. Raising and lowering wind speed readings by 1.0 m s^{-1} increased and decreased evaporation rates by 20%. The response to a 0.5°C increase in air temperature was an 8% decrease in evaporative water loss, and the response to a 0.5°C increase in water temperature was an 11% increase in the evaporation rate.

RESULTS—*Northern Florida Bay*—Weather conditions recorded during the December–March field study in northern Florida Bay were typical of winter months, but variable as a result of frontal passages. Mean values of variables used in the evaporation calculations are summarized in Table 1. The average air-water temperature difference was only −0.1°C at the John-

TABLE 1. Mean values of wind speed (S), air temperature (T_a), water temperature (T_w) and relative humidity (H) used in evaporation calculations; and mean evaporation rates (E). Wind speed, in m s^{-1}, is corrected to the 10-meter level; air and water temperatures are in °C, and relative humidity is in percent. Evaporative water loss is in cm h^{-1}.

	S	T_a	T_w	H	E
1. Northern Florida Bay					
a. Johnson Key	5.7	22.2	22.3	77.2	0.015
b. Butternut Key	5.6	22.7	22.0	77.4	0.012
2. Southern Florida Bay C-MAN Station					
a. July–December 1998	5.4	27.4	28.3	75.7	0.024
b. February–July 1999	5.0	24.6	26.2	75.1	0.023

son Key study site, indicating near-neutral stability in the lowest layer of the atmosphere. The root-mean-square (rms) deviation about the average was 1.7°C. At the Butternut Key study site, the mean +0.7° air-water temperature difference indicates stable conditions, but the rms deviation was 2.2°C, and thus both unstable and more stable conditions existed during the study. Mean wind speeds at Johnson Key and Butternut Key were 5.7 and 5.6 m s^{-1}, with rms deviations of 2.8 and 3.0 m s^{-1}, respectively. Light wind conditions were infrequent at both locations, with wind speeds less than 1 m s^{-1} in only 2% of the observations.

Day-to-day fluctuations in evaporation rates at the Johnson Key and Butternut Key weather stations are shown in Figure 2. In both plots, high-frequency variations are prominent, and the magnitude of peak values is highly variable. During periods of strong winds, instability in the lowest layers of the atmosphere and/or low humidity, evaporation rates can exceed 0.05 cm h^{-1} at Johnson Key and 0.06 cm h^{-1} at Butternut Key. For much of the record, however, evaporative water loss does not exceed 0.02 cm h^{-1} at Johnson Key and 0.01 cm h^{-1} at Butternut Key. Mean evaporation rates in the Johnson Key and Butternut Key records are 0.015 and 0.012 cm h^{-1}, respectively, and the rms deviations from the means are 0.011 and 0.012 cm h^{-1}. Some features appear in both plots, such as the times of highest evaporation rates and periods of sustained high evaporation. The correlation coefficient of Johnson Key and Butternut Key evaporation rates, calculated from the period of overlap, is +0.78, indicating that 61% of the variability in evaporation at one study site is associated with the variability recorded at the other.

A diurnal variation in evaporation is poorly defined at the Johnson Key site, and it is missing at the Butternut Key study site. The autocorrelation coefficient calculated for a time lag of 24 hours was 0.44 for the Johnson Key data. This is only slightly higher than values found for shorter and longer time lags. Autocorrelation for time lags of 20 and 30 hours is 0.36 and 0.15, respectively. The autocorrelation coefficient at a period of 24 hours is +0.33 for the Butternut Key data, and this value is part of a steady

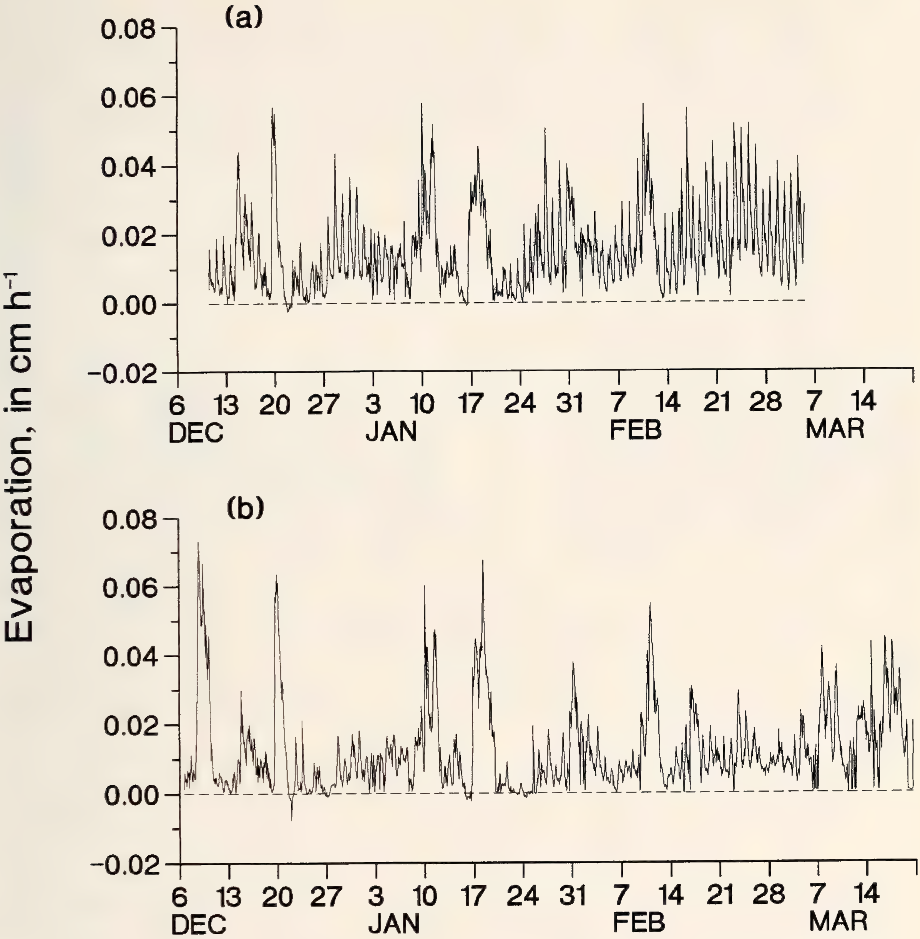

FIG. 2. Hourly evaporation rates, in cm h^{-1}, at (a) Johnson Key, December 10, 1996, to March 5, 1997, and (b) Butternut Key, December 6, 1996, to March 20, 1997.

decrease for lags of between 20 hours (0.40) and 30 hours (0.19). Buys-Ballots averaging of hourly evaporation rates identified a weak diurnal signal in both time series, but with distinct differences in highest evaporation rates and in times of minimum values. At both study sites, evaporation was greatest from 1500–1800 EST. At Johnson Key, however, the late afternoon evaporation rate was approximately 0.023 cm h^{-1}, while at Butternut Key the value was approximately 0.015 cm h^{-1}. Minimum evaporation rates were approximately 0.011 cm h^{-1} at both locations. However, at Johnson Key lowest values occurred between 0700 and 1000 EST, while at Butternut Key minimum values were broadly distributed from 2300 to 0900 EST.

Figure 3 shows the P-E balance for Johnson Key (a) and Butternut Key (b) during the December to March winter study period. Both plots show a net freshwater loss and similar ending values, but significant differences

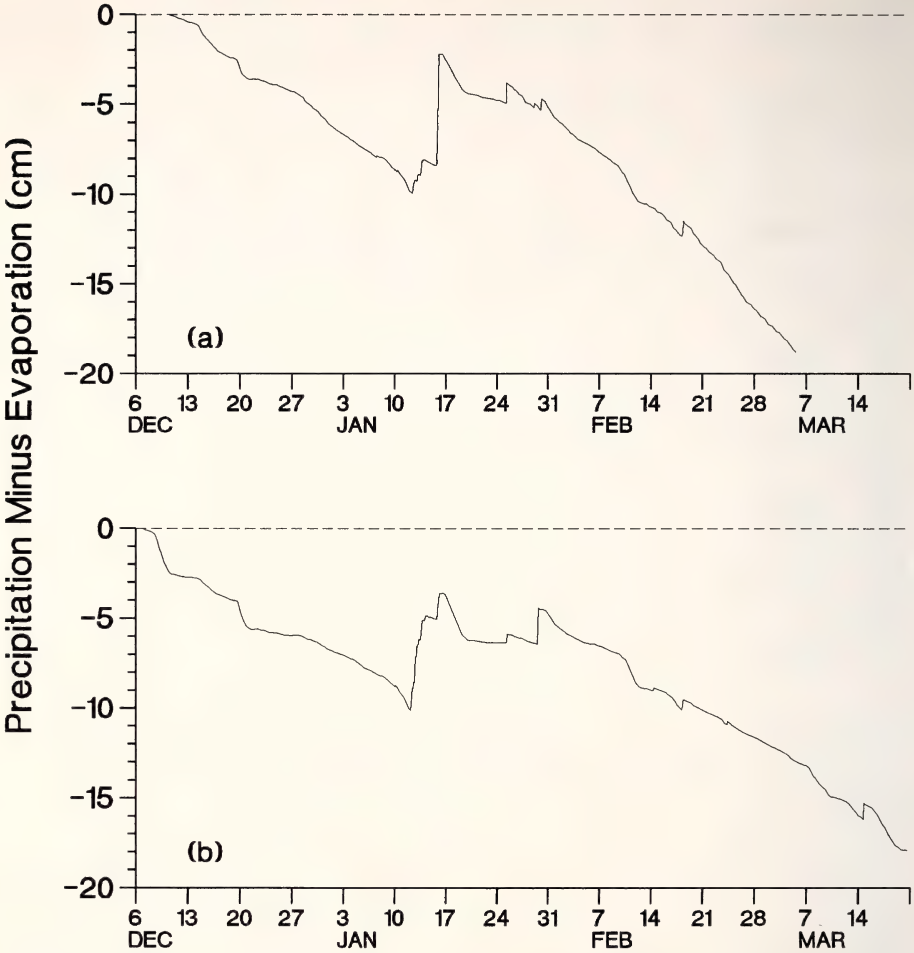

FIG. 3. Cumulative precipitation minus evaporation at (a) Johnson Key, December 10, 1996, to March 5, 1997, and (b) Butternut Key, December 6, 1996, to March 20, 1997. Negative values indicate a net water loss.

appear in the details. While both plots indicate large rainfall gains at the midpoint of the study, the sharp rise in the plot of the Butternut Key data occurs four days before the rise recorded in the Johnson Key data. Rain showers are recorded at both weather stations on January 12 and 16. At Johnson Key heavier rainfall is recorded on January 16, while at Butternut Key the larger amount was received on January 12.

Southern Florida Bay—With the exception of the passage of Hurricane Georges on September 25, weather conditions during the two studies were typical of the times of year during which data were collected (Table 1). Air and water temperatures from the first study period indicate that the water

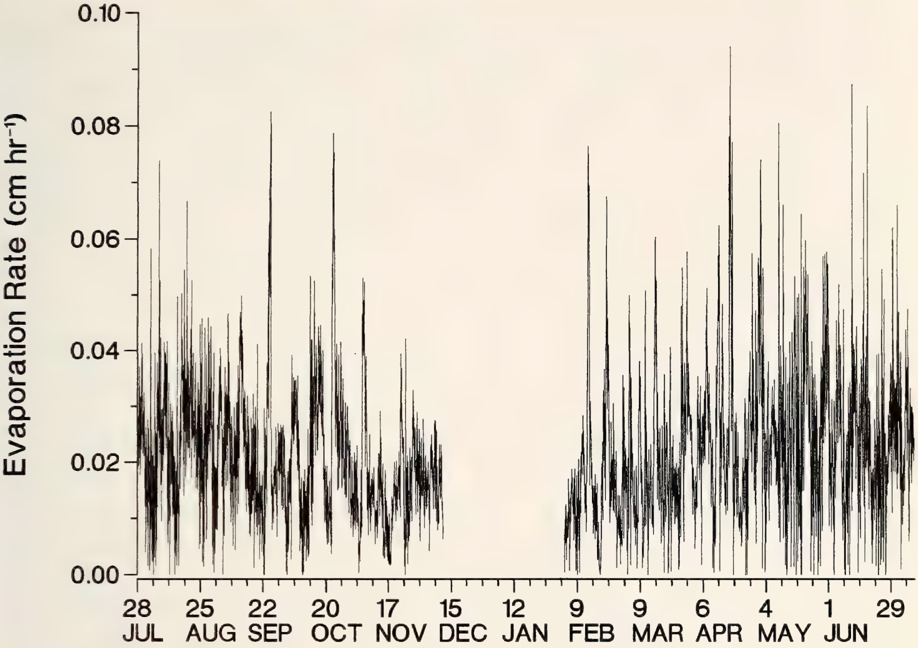

FIG. 4. Evaporation rates, in cm h^{-1}, at the Coastal-Meteorological Automated Network weather station, July 28 to December 11, 1998, and February 3 to July 9, 1999.

was 1°C warmer than the air on average. This unstable condition was variable however. The rms air-water temperature difference was 1.5°C. During the February–July field study, air and water temperatures were slightly lower, but both the instability and the fluctuations about the mean increased. The mean air-water temperature difference was −1.6°, and the rms temperature difference was 2.2°C. Mean wind speeds and relative humidities were nearly the same during the two field studies, and differences were within the accuracies of the recording instrumentation. Light wind conditions were rare, with speeds less than 1 m s^{-1} only 4% of the time during the first study and 5% of the time during the second.

Hourly evaporation rates calculated from the C-MAN data are shown in Figure 4. High-frequency fluctuations are the dominant feature of the plot, but they are superimposed onto lower-frequency variations associated with the day-to-day movement of weather systems through the study area. The mean evaporative water loss during the first, 135-day study is 0.024 cm h^{-1}. During the second, 156-day study, the mean evaporative loss is 0.023 cm h^{-1}. The rms deviation from the means during the two field studies are 0.011 and 0.013 cm h^{-1}. Evaporation rates at the C-MAN station decrease to near-zero levels much less often, and values are generally between 0.01 and 0.04 cm h^{-1}. Evaporation rates in excess of about 0.08 cm h^{-1} occur infrequently. Low-frequency variations, representing alternating periods of high and low wind speed, clear and cloudy skies and relatively high and low humidity are apparent, especially during late summer and fall months.

Buys-Ballots averaging of the first 135 days of data indicates that the diurnal variation of evaporation embedded within the high-frequency fluctuations varies from 0.022 to 0.026 cm h^{-1}. Highest evaporation rates occur from about 1900 to 0400 EST, and lowest evaporation rates occur from about 0900 to 1500 EST. Autocorrelation coefficients do not peak at the diurnal periodicity. Autocorrelations at periods of 20, 24 and 30 hours are 0.44, 40 and 0.29, respectively. Analysis of evaporation rates from the second part of the time series produced similar results. Maximum evaporation occurred between 2200 and 0300 (0.026 cm h^{-1}), and minimum evaporation occurred from 1000 to 1800 EST (0.021 cm h^{-1}). Autocorrelation coefficients decreased steadily and did not peak at a period of 24 hours.

Evaporation is influenced by several factors, but a close look at wind speed in particular helps explain why the diurnal fluctuation of evaporation is so poorly defined. Because of the longer record from the C-MAN weather station, and because of the more frequent checks of the relative humidity sensor, data from that location were used to investigate the diurnal cycle. For this purpose, the two records were combined, and the total number of diurnal cycles increased to 291. The difference between the strongest and weakest winds on an average day was about 1 m s^{-1}. Strongest wind speeds in the Buys-Ballots average cycle were about 5.3 m s^{-1} and occurred during the seven-hour time period from 1900 and 0100 EST. Lowest wind speeds of about 4.4 m s^{-1} occurred at 1300 EST. The scatter is large relative to the range of the means. The rms deviation from both the average maximum and average minimum wind speeds was 2.7 m s^{-1}. The diurnal variation in the specific humidity gradient (not shown) is well defined, but it is significantly shifted in time relative to the diurnal variation in wind speed. Highest humidity gradients occur around 1600 EST, 3–9 hours before strongest wind speeds are recorded. Lowest humidity gradients occur at 0500–0600 EST, 7–8 hours before weakest wind speeds. Thus, the poorly defined diurnal variation of evaporation and the low autocorrelation at a period of 24 hours are because the two factors most important in controlling evaporation are significantly out of phase within the diurnal cycle.

Comparison of C-MAN water temperatures recorded approximately 1 m below the surface and buoy temperatures recorded 5 cm below the surface suggest that near-surface vertical temperature gradients are minimal at the site study in southern Florida Bay. The mean water temperatures calculated from the C-MAN and buoy data were 29.6° and 29.7°C, respectively. Given the accuracies of these two readings, the means can be considered identical. The rms temperature difference, however was 1.3°C.

Table 2 summarizes results from northern and southern Florida Bay by listing monthly mean evaporative water losses, expressed in cm d^{-1}. Results from the four seasonal studies do not add up to a full year, some means are based on incomplete months, and interannual variability is unknown. Thus,

TABLE 2. Monthly mean evaporative water loss, in cm d^{-1}. When full months were not available for the calculations, the number of days appears in parentheses.

Month	Johnson Key	Butternut Key	C-MAN Station	C-MAN Station
January	0.342	0.271		
February	0.427	0.267		0.399 (25)
March	0.430 (5)	0.368 (20)		0.482
April				0.598
May				0.649
June				0.560
July			0.750 (3)	0.613 (9)
August			0.700	
September			0.614	
October			0.610	
November			0.412	
December	0.285 (21)	0.268 (25)	0.413 (11)	

neither the annual cycle nor an annual total can be obtained from the available data base. Nevertheless, the available data provide useful information regarding spatial variability and cumulative water loss. For example, in nearly all months for which data are available both from the two study sites in northern Florida Bay and (from different years) the study site in southern Florida Bay, mean evaporative losses in northern Florida Bay are about 78% of those estimated for the southern part of the bay. Also, though a full year of measurements is not available from any location, the nearly 292 days of data from the C-MAN study site can be combined, and the 163 cm total water loss at that location is probably representative of the deeper waters of southern Florida Bay for the same time period.

DISCUSSION—The data base assembled from these two field studies provides an introduction to evaporative water losses from Florida Bay that covers both summer and winter seasons, and it provides preliminary numbers to use for comparisons with other gains and losses of fresh water. Results suggest that 0.023 cm h^{-1}, or approximately 0.5 cm d^{-1}, is a representative number to use for evaporation in the southern part of the bay. A lower value of about 0.3 cm d^{-1} may be more appropriate for the northern part of the bay, although this might apply only to the winter season. Results from all three stations show prominent but highly variable high-frequency fluctuations and virtually no consistent diurnal signal embedded in the high-frequency variability. The poorly-defined diurnal variation in evaporation is partly a result of the weak diurnal fluctuation in wind speed, and partly a result of different times of strongest winds and maximum humidity gradients.

It is likely that evaporation from the southern part of Florida Bay is distinctly different from that occurring in the northern part, because water depth in the southern part of the bay is generally deeper. Studies have not been conducted to confirm that water temperatures in the shallower and more isolated northern part of the bay are significantly different, but it is likely that seasonal differences occur. In summer months, the shallow waters in the northern part of the bay probably reach a higher temperature, and in winter months the northern part of the bay is probably cooler at least immediately following cold-air outbreaks. If so, then evaporation could be appreciably higher in summer in the northern part of the bay, especially over the shallow mud banks. The topic of spatial and seasonal variations in evaporation, and thus in the precipitation-evaporation balance should receive attention in follow-up studies.

An estimation of the uncertainty of evaporative loss calculations is difficult, because there is no standard against which results can be compared. In many previous studies based on bulk aerodynamic formulas, a potentially large source of error was the Dalton Number selected for use in Equation (1). Hsu (1978) and Brutsaert (1982) summarized Dalton numbers from many previous studies. Values range from 1.1 to 1.47×10^{-3}, and most recommended mean values are accompanied by a large standard deviation. E.g., Pond and co-workers (1974) suggested $1.41 \pm 0.18 \times 10^{-3}$. The range of 1.1 to 1.5×10^{-3}, expanded further by the standard deviations, suggests that errors as large as ±20–30% may be common if a constant value of C_E is used in the calculations. The approach used here, however, is based on a variable Dalton Number that is a function of both wind speed and the stability of the lowest layers of the atmosphere (Smith, 1988). The Dalton Numbers used for the Johnson Key and Butternut Key data averaged 1.42 and 1.35, and the standard deviations about the means were 0.19 and 0.24 $\times 10^{-3}$, respectively. Similarly, the 1.57 and 1.58×10^{-3} mean values found for the C-MAN data both had standard deviations of 0.28×10^{-3}. While the uncertainty associated with the estimates of evaporative water loss cannot be quantified, it is likely that it is considerably less than the uncertainty that accompanies the decision to use a constant Dalton Number.

The 163 cm evaporative water loss calculated from the 291 days of data from southern Florida Bay is nearly equal to the 162 cm annual loss calculated for Lake Okeechobee by Morton (1986). Mean wind speeds in the interior of the state may be lower than those occurring in Florida Bay, however. More significantly, the evaporative water loss found for a nine-month time period in this study is considerably higher than the 110 cm annual total found by Nuttle and co-workers (in review) using a mass-balance approach. Their study was restricted to the shallower northern and eastern parts of the bay, however. Before annual evaporative losses can be determined for the entire bay, data must be obtained over several full-year time periods, and measurements must be made at several locations representing both the shallower, northern and eastern parts of the bay and the deeper, southern and western parts of the bay.

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THE HERPETOFAUNA OF EVERGLADES NATIONAL PARK

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ABSTRACT: *An inventory of amphibians and reptiles is provided for Everglades National Park (ENP), with special attention to temporal changes associated with the list. The 55 native, non-marine species in ENP comprise 40.4% of the entire native non-marine Florida herpetofauna, whereas 21.1% of Florida's exotic species occur in ENP. The native herpetofauna of ENP is comprised mostly of southeastern U.S. coastal plain species at the southern end of their geographic ranges, and is best represented by snakes and anurans. The status of ten species recorded in areas near the park, but not within the park, remains in question. Taxonomic uncertainties are identified in four polytypic species found in the park. Past changes in, and future predictions regarding, the Park's herpetofauna are associated with activities of humans. In the past 40 years, three species have disappeared from ENP, and six exotic species, mostly lizards, have invaded the park. Changes in species abundance, more than the presence/absence of strongly aquatic and upland species, are predicted to occur following proposed hydrological changes in ENP. New exotic species are likely to appear in ENP because of increases in human traffic in Dade County and the influx of exotic species in southern Florida.*

EVERGLADES National Park (ENP) is a 0.9 million hectare wilderness established as a National Park in 1947. The park is bordered on the north by Big Cypress National Preserve (BNP) and Tamiami Trail and extends to the mangrove-lined west coast of Florida. Much of Florida Bay is within the southern park boundaries which follow the inside alignment of the upper and middle Florida Keys. The congressionally authorized expansion area brings the park boundary to the L-31 canals on the east to include northeast Shark Slough. Wetland habitats comprise the freshwater and saline glades of the park. The park also includes one of the most extensive mangrove swamps on Earth (Fig. 1).

The first published reports of the composition and distribution of the amphibians and reptiles of southern Florida included the region of ENP before its dedication as a National Park in 1947 (Cope, 1888; Lonnberg, 1894; Cope, 1900; Brimley, 1910; Safford, 1919, Barbour, 1920; Deckert, 1921,1922). Carr (1940) provided a relatively complete summary of the distribution of amphibians and reptiles in southern Florida, listing records for 162 species and subspecies for the entire state by county. His accounts

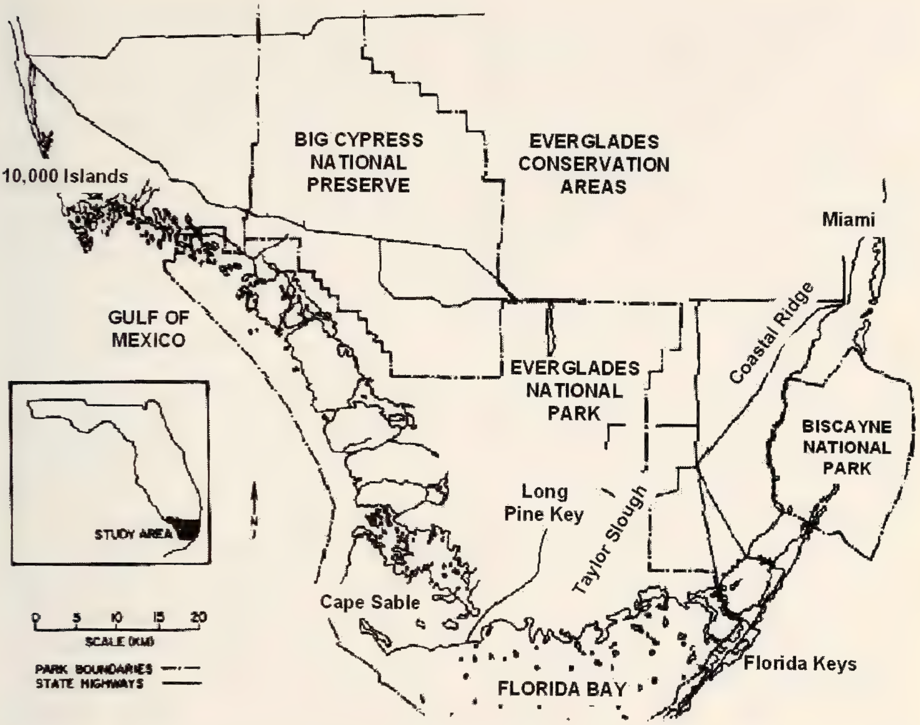

FIG. 1. A map depicting the boundaries of Everglades National Park with relevant features of the park.

presented general ecological data on habits, habitat, abundance, feeding, and reproduction of the Florida herpetofauna. Carr (1940) documented all of the presently known native species from extreme southern Florida (Dade and Monroe County), except for *Nerodia taxispilota,* first reported from southern Florida by Schwartz (1950), and *Chelydra serpentina,* first reported from southern Florida by Duellman and Schwartz (1958). Carr and Goin (1959) updated some herpetological information from Carr's 1940 work and provided identification keys to the species.

The study by Duellman and Schwartz (1958) stands as the most comprehensive work on the herpetofauna of southern Florida. The monograph included detailed data on taxonomy, general ecology, and distribution for 80 species of reptiles and amphibians, including data from several collecting localities within ENP. Approximately thirty years later, the snake community of Long Pine Key was studied (Steiner, 1987; Dalrymple et al., 1991a,b) and a discussion of the herpetofauna of that area was provided (Dalrymple and Steiner, 1988). Dalrymple (1988) produced a comprehensive ecological and biogeographical study of the Long Pine Key herpetofauna, with emphasis on habitat use. Zoogeography of the Florida herpetofauna (Carr, 1940; Neill, 1957; Duellman and Schwartz, 1958; Dalrymple, 1988) and the exotic herpetofauna of Florida (Wilson and Porras, 1983; Butterfield et al., 1997; Meshaka et al., 2000) have also been investigated.

Other publications on the southern Florida herpetofauna include those for amphibians (Brady and Harper, 1935; Weber, 1944; Goin, 1947; Schwartz, 1952; Schwartz and Duellman, 1952; Allen and Neill, 1953; Neill, 1958; Moler and Keezer, 1993; Machovina, 1994; Meshaka, 1994; Butterfield et al., 1997; Meshaka and Jansen, 1997; Meshaka, 1999a,b; Meshaka et al., 2000; Meshaka and Woolfenden, 1999) and reptiles (Babis, 1949; Neill, 1949; Allen and Neill, 1950; Dowling, 1950; Schwartz, 1950; Babbitt and Babbitt, 1951; Auffenberg and Babbit, 1953; Schwartz, 1955; Uzell and Schwartz, 1955; Allen and Neill, 1957; Neill, 1958; Telford, 1966; Craighead, 1968; Franz, 1977; Iverson, 1978a,b; Porras and Wilson, 1979; Christman, 1980; Dalrymple, 1980; Telford, 1980; Steiner, 1981; Auffenberg and Franz, 1982; Dalrymple et al., 1985; Lee, 1985; Steiner, 1985; Meshaka, 1989, 1991, 1994; Butterfield et al., 1997; Meshaka, 1999a,b; Meshaka and Deyrup, 1999; Meshaka, 2000; Meshaka et al., 2000).

ENP personnel produced two herpetofaunal checklists in 1968 and 1984. The National Park Service conducted and sponsored research on threatened and endangered species, such as crocodilians (Moore, 1953; Kushlan, 1974; Ogden, 1978; Hall et al., 1979; Menzies et al., 1979; Kushlan, 1980; Kushlan and Kushlan, 1980a,b; Mazzotti, 1983; Lutz and Dunbar-Cooper, 1984; Mazzotti et al., 1988; Kushlan and Mazzotti, 1989a,b), *Caretta caretta* (Klukas, 1967; Davis and Whiting, 1977; Steiner and Bass, 1980), *Gopherus polyphemus* (Kushlan and Mazzotti, 1982), and *Drymarchon corais couperi* (Steiner et al., 1983).

Yet, despite extensive herpetofaunal studies in southern Florida and ENP since the turn of the century, no recent herpetofaunal analysis exists for ENP. The need for such an inventory is critical in light of the profound changes that have occurred in southern Florida since the last complete herpetofaunal list was compiled (Duellman and Schwartz, 1958). For example, since the 1950s southern Florida has experienced three major hurricanes (Donna-1960, Betsy-1965, Andrew-1992), the loss of contiguous habitat to development, and increasing establishment and within-state dispersal of exotic species of reptiles and amphibians. In addition, south Florida is the site of the largest ecosystem restoration program in history, which will result in more change to the herpetofauna. For these reasons, we provide an updated herpetofaunal inventory of ENP. We compare our list with that of Duellman and Schwartz (1958) from ENP and southern Florida, and consider the future of the fauna in light of actual and proposed human-mediated changes in the south Florida landscape.

METHODS—This inventory is based on scientific and technical literature citations, specimens housed in the Everglades Regional Collections Center (ERCC) in ENP, the Florida Museum of Natural History, and the Carnegie Museum of Natural History. Scientific, to the level of subspecies, and common names follow Collins (1997) unless there are more recent changes;

such changes are noted in the species accounts. Because of significant changes in the taxonomic status at the level of species and subspecies in the Florida herpetofauna over the past fifty years, faunal comparisons are made at the species level, unless otherwise noted.

STUDY AREA—Three major habitat divisions are represented in ENP. Freshwater habitats include a variety of vegetation communities along a hydroperiod gradient that ranges from flooding for a short period each year to year-round inundation. Because of the low topographic elevations and high annual rainfall, such habitats comprise much of the park's interior. Sawgrass (*Cladium jamaicense*) marshes are the most extensive habitat, and are interspersed by wet prairie and slough communities of various aquatic plant genera (e.g., *Eleocharis, Rhynchospora, Panicum, Nymphaea,* and *Utricularia*). Floating mats and epiphytic growths of algae (periphyton) are common features. Ponds excavated by the American alligator (*Alligator mississippiensis*) provide deeper, open-water habitat and dry-season refuges and feeding sites for other reptiles and amphibians. Extensive man-made canals and borrow ponds play a similar role. Dense beds of native and introduced plants like *Hydrilla,* water hyacinth (*Eichhornia crassipes*), and waternaiad (*Najas*) are home to several members of the herpetofauna. Along the edges of the main Everglades sloughs, seasonally flooded prairies of *Muhlenbergia* grass, with many limestone solution holes, are also used by the herpetofauna. In addition to the graminoid wetlands, an area of dwarf cypress forest (*Taxodium* spp.) is present to the west of Taylor Slough.

Upland habitats of the park are infrequently inundated. However, there are usually numerous, flooded solution holes in those habitats that support some aquatic species. Tropical hardwood hammocks in ENP contain dozens of species of West Indian and North American hardwood trees, including live oak (*Quercus virginiana*), gumbo-limbo (*Bursera simarubra*), pigeon-plum (*Cocoloba diversifolia*), and strangler fig (*Ficus aurea*). Fires do not often burn into hammocks, allowing the development of organic soils covered by leaf litter. Rockland pinewoods of slash pine (*Pinus elliottii* var. *densa*) occur on Long Pine Key. The tropical hardwood understory beneath the pines is controlled by periodic fires which also consume detritus on the pine-forest floor. Common associated plants are saw palmetto (*Serenoa repens*), rough velvetseed (*Guettarda scabra*), poisonwood (*Metopium toxiferum*), and the grasses, *Andropogon* and *Aristida.* A third upland community is a disturbance-produced association of Brazilian pepper (*Schinus terebinthefolius*) with wax myrtle (*Myrica cerifera*) and saltbush (*Baccharis halimifolia*). This association occurs on former agricultural lands called the "Hole-in-the-Donut" on Long Pine Key. Brazilian pepper is also invasive in pineland and mangrove/coastal prairie habitats.

The shallow, marine waters of Florida Bay contain extensive seagrass meadows of *Thalassia, Halodule, Syringodium,* and associated algae. The seagrass beds and mudflats are dissected by a network of deeper basins and channels through which tidal interchange occurs. Tidal amplitude is generally small and is easily overwhelmed or compounded by the effects of wind. Most of the shoreline of the keys and the mainland is edged by red mangroves (*Rhizophora mangle*), black mangroves (*Avicennia germinans*), white mangroves (*Laguncularia racemosa*), and buttonwood (*Conocarpus erectus*). Expanses of coastal prairies are characterized by the genera *Spartina, Distichlis, Batis,* and *Salicornia.* Sandy beaches and substrates are localized, the largest expanses occurring on Cape Sable and Highland Beach. Oyster bars are common in the Ten Thousand Islands region and south to Shark River. Reef-building corals are absent from ENP, although some hard bottom with soft corals exists in southern Florida Bay. Inland from the coast lies a network of mangrove-lined bays, rivers, and creeks that drain the freshwater marshes of the Everglades. Salinity in those channels fluctuates seasonally and annually.

RESULTS AND DISCUSSION—*Species composition*—The total number of non-marine species of amphibians (N = 16) and reptiles (N = 47) in ENP represents a subset of the non-marine amphibian (N = 21) and reptile (N = 60) species of southern Florida (Tables 1, 2) documented by Duellman and

Schwartz (1958). The native non-marine species of amphibians (N = 14) and reptiles (N = 41) in ENP represent an even smaller subset of the native non-marine species of amphibians (N = 53) and reptiles (N = 83) in Florida (Moler, 1990; Moler and Keezer, 1993). One reason for this disparity between the native herpetofauna of ENP and Florida is that northern and central Florida represent the southern terminus of the geographic ranges for many species. The balance, with the exception of *Sphaerodactylus notatus* and *Crocodylus acutus,* range within the southeastern coastal plain and their geographic ranges terminate in extreme southern Florida. In addition, habitats and climate of the Everglades may be unsuitable for species of plethodontid and ambystomatid salamanders that are found farther north (Dalrymple, 1988). That factor, and slow post-glacial dispersal, are plausible explanations for low species diversity of salamanders in ENP.

The four salamanders that inhabit ENP represent 6.4% of the park's non-marine herpetofauna (Table 1). All native species, the salamanders of ENP comprise only 15.4% of the 26 species found in Florida (Moler, 1990; Moler and Keezer, 1993). The four species in ENP appear to remain aquatic throughout their lives, with two (*Siren* and *Pseudobranchus*) retaining larval traits such as external gills even as reproductive adults. *Notophthalmus viridescens piaropicola* commonly metamorphoses through a sub-adult terrestrial stage, an Eft, throughout most of its eastern U.S. range. Although only one Eft has been found in southern Florida (in Big Cypress National Preserve; Duellman and Schwartz, 1958), adults with neotenic characteristics are not uncommon (Duellman and Schwartz, 1958). Three of the ENP salamanders are widely distributed in the southeastern coastal plain; however, *P. striatus* is restricted to peninsular Florida and the southern parts of Georgia and South Carolina. The subspecies *P. s. belli* (type locality—Tamiami Canal), now *P. axanthus belli* (Moler and Keezer, 1993), is restricted to the Everglades region (Schwartz, 1952).

Twelve species of frogs (N = 10) and toads (N = 2) inhabit ENP and represent 19.1% of the park's non-marine herpetofauna (Table 1). The ten native species comprise 37.0% of the 27 native anuran species that occur in Florida (Moler, 1990). Hylidae is the most speciose family of native anurans in ENP, represented by five species. With the exception of *Rana sphenocephala* and *Gastrophryne carolinensis,* the native anurans of ENP are southeastern coastal plain species near the end of their geographic ranges in extreme southern Florida. Although no subspecies of anuran is endemic to the southern Everglades, the type locality for the *Pseudacris nigrita verrucosa* is Royal Palm Hammock (Brady and Harper, 1935).

Eleven native species of non-marine turtles inhabit ENP and represent 17.5% of the park's non-marine herpetofauna (Table 1). All are native in ENP and comprise 55.0% of the 20 native non-marine turtle species that occur in Florida (Moler, 1990). Most of the non-marine turtles in ENP are widely distributed along the southeastern U.S. coastal plain, except for two

TABLE 1. Habitat associations of amphibians and reptiles from Everglades National Park.

Species	Slough	Canal	Sawgrass marsh	Wet prairie	Pond	Lake	Coastal prairie	Solution hole	Rockland pinewoods	Hardwood hammock	Schinus	Building	Mangrove forest	Dune	Estuarine	Marine	Total
Amphiuma means		X	X														2
Notophthalmus viridscens piaropicola			X					X									2
Siren lacertina			X		X												2
Pseudobranchus axanthus belli			X														1
Gastrophryne carolinensis			X	X					X	X	X		X				6
Rana grylio	X	X	X		X	X											5
Rana sphenocephala	X	X	X	X	X	X				X	X		X				9
Bufo quercicus			X						X	X							3
Bufo terrestris			X						X	X	X						4
Acris gryllus dorsalis	X	X	X		X			X									5
Hyla cinerea	X	X	X		X	X			X	X	X	X	X				10
Hyla squirella	X	X	X	X	X	X			X	X	X	X					10
*Osteopilus septentrioinalis****	X	X			X	X			X	X	X	X	X				9
Pseudacris nigrita verrucosa									X	X							2
Pseudacris ocularis			X														1
*Eleutherodactylus planirostris planirostris****									X	X			X				3
Chelydra serpentina osceola	X		X					X									3
Deirochelys reticularia chrysea	X		X		X												3
Malaclemmys terrapin macrospilota															X		1
M. t. rhizophorarum															X		1
M. t. tequesta															X		1
Pseudemys floridana floridana	X	X	X					X									4
P. nelsoni	X	X	X														3
Terrapene carolina bauri				X					X	X							3

TABLE 1. Continued.

Species	Slough	Canal	Marsh	Prairie	Pond	Lake	Coastal prairie	Solution hole	Pineland	Hammock	Schinus	Building	Mangrove forest	Dune	Estuarine	Marine	Total
Gopherus polyphemus									X						X		2
Kinosternon baurii	X	X	X		X	X										X	6
K. subrubrum steindachneri			X														1
Sternotherus odoratus		X	X														2
Apalone ferox	X	X	X		X	X											5
*Caretta caretta***																X	1
*Chelonia mydas***																X	1
*Eretmochelys imbricata imbricata***																X	1
*Lepidochelys kempii***																X	1
*Dermochleys coriacea***																X	1
*Gekko gecko****												X					1
*Hemidactylus garnotii****												X					1
*H. mabouia****												X					1
Sphaerodactylus notatus notatus									X	X							2
Anolis carolinensis	X		X	X					X	X		X	X				7
*A. sagrei****									X	X		X	X				4
Scincella lateralis				X					X	X							3
Eumeces inexpectatus			X	X					X	X	X	X	X				7
Ophisaurus compressus			X	X					X								3
*Ramphotyphlops braminus****											X						1
*Python molorus bivittatus****													X				1
Cemophora coccinea coccinea									X	X			X				3
Coluber constrictor paludicola	X	X	X	X	X	X			X	X	X		X				10
Diadophis puncatus punctatus								X	X	X						3	
*Drymarchon corais couperi***								X	X			X	X			4	

TABLE 1. Continued.

Species	Slough	Canal	Marsh	Prairie	Pond	Lake	Coastal prairie	Solution hole	Pineland	Hammock	Schinus	Building	Mangrove forest	Dune	Estuarine	Marine	Total
Elaphe guttata guttata									X	X	X	X	X				5
*E. obsoleta quadrivittata**									X	X	X	X	X				5
*E. obsoleta rossalleni**									X	X	X	X	X				5
Farancia abacura abacura	X	X	X														3
Lampropeltus getula floridana			X							X	X						3
L. triangulum elapsoides							X		X	X							3
Nerodia clarkii compressicauda						X							X		X	X	4
N. fasciata pictiventris	X	X	X	X	X	X											6
N. floridana	X	X	X		X	X											5
N. taxispilota	X				X												2
Opheodrys aestivus									X	X	X						3
Regina alleni	X	X	X														3
Seminatrix pygea cyclas	X	X	X														3
Storeria dekayi victa									X	X	X						3
*Thamnophis sauritus nitae**			X	X													2
*T. s. sackenii**			X	X													2
*T. sirtalis similis**				X					X	X							3
*T. s. sirtalis**				X					X	X							3
Micrurus fulvius fulvius									X	X							2
Agkistrodon piscivorus conanti			X	X	X						X		X				5
Crotalus adamanteus							X		X	X	X		X	X			6
Sistrurus miliarius barbouri				X			X		X	X	X						5
Alligator mississippiensis	X	X	X		X	X									X		6
*Crocodylus acutus***															X	X	2
Total	21	19	35	16	16	12	3	4	31	31	19	12	18	3	7	6	

* = Morphological characteristics of more than one subspecies present.
** = Federal T&E species.
*** = Exotic species.

TABLE 2. Herpetofauna of southern Florida exclusive of Everglades National Park (Duellman and Schwartz, 1958).

Species	Introduced
Scaphiopus holbrookii	
Rana capito aesopus	
Bufo marinus	X
Hyla femoralis	
Hyla gratiosa	
Gonatodes albogularis fuscus	X
Hemidactylus turcicus	X
Sphaerodactylus argus argus	X
Sphaerodactylus elegans elegans	X
Anolis distichus	X
Leiocephalus carinatus armouri	X
Sceloporus woodi	
Eumeces egregius egregius	
Eumeces egregius onocrepis	
Eumeces laticeps	
Neoseps reynoldsi	
Ameiva ameiva	X
Cnemidophorus sexlineatus sexlineatus	
Ophisaurus attenuatus	
Coluber constrictor priapus	
Masticophis flagellum flagellum	
Tantilla oolitica	

species, *Pseudemys nelsoni* and *Apalone ferox,* whose geographic ranges extend little beyond Florida.

Nine species of lizards inhabit ENP and represent 14.3% of the park's non-marine herpetofauna (Table 1). The five native species in ENP comprise 29.4% of the 17 native lizards (including amphisbaenians) that occur in Florida (Moler, 1990). Five native species range throughout Florida and the southeastern U.S. coastal plain, but *Sphaerodactylus notatus* is limited to southern Florida, Cuba, and the Bahamas. *Eumeces inexpectatus* and *Anolis carolinensis* are the two most widespread lizards in the park.

The two native species of crocodilians occurring in Florida (Moler, 1990) inhabit ENP and represent 3.2% of the park's non-marine herpetofauna (Table 1). *Alligator mississippiensis,* with a distribution that includes much of the southeastern United States, is found throughout the park where it is at the southern end of its geographic distribution (Conant and Collins, 1991). The geographic range of *Crocodylus acutus* reaches its northern boundary in southern Florida. In ENP, it occurs along northern Key Largo, Florida Bay, Cape Sable, and the interior lakes at the southern end of the park.

Twenty-five species of snakes inhabit ENP and represent 39.7% of the park's non-marine herpetofauna (Table 1). The twenty-three native species comprise 52.3% of the 44 native snake species in Florida (Moler, 1990). All of the ENP species occur throughout Florida, and many range throughout much of the United States. However, two recognized subspecies, *Coluber constrictor paludicola* (Type locality: Kendall, Dade County), and *Elaphe obsoleta rossalleni* (Type locality: Broward County) are endemic to the Everglades region (Duellman and Schwartz, 1958). Only two species, *Regina alleni* and *Seminatrix pygaea cyclas,* are primarily restricted to Florida. Only *Drymarchon corais* is primarily a neotropical species, ranging south to Argentina; *Drymarchon c. couperi* is found in the southeastern United States where it replaces the western form, *D. c. erebennus* (Conant and Collins, 1991). Of the park herpetofauna, *Lampropeltus triangulum elapsoides* is geographically the most widely distributed snake species; milk snakes range from Ontario to Ecuador. *Nerodia clarkii compressicauda,* of the southern United States, is also found in Cuba (Conant and Collins, 1991).

Exotic species—Exotic species of amphibians (N = 2) and reptiles (N = 6) in ENP comprise only 12.7% of the total number of non-marine park species, and represent one half of the exotic amphibians and 17.7% of the exotic reptiles (exclusive of *Trachemys scripta elegans* which is exotic to southern Florida) recorded from Florida as a whole. This suggests that, thus far, invasion by exotics in the park has been limited. However, this apparent resistance may reflect the fact that many of the newly established species have not yet had time to disperse into the park (Butterfield et al., 1997; Meshaka et al., 2000).

Two of the introduced species, *Osteopilus septentrionalis* and *Eleutherodactylus planirostris planirostris,* are firmly established and widely distributed in ENP, and were present in southern Florida before 1900 (Meshaka et al., 2000).

Four of the 31 exotic lizards found in Florida (Meshaka et al., 2000) occur in ENP, and three of these are geckos, which appear to be restricted, or nearly so, to buildings and disturbed sites (Meshaka, 2000; Meshaka et al., 2000). The fourth species, *Anolis sagrei,* has probably been in the park since the 1960s and is present in all upland habitats.

Both exotic species of snakes that are established in Florida inhabit ENP (Meshaka et al., 2000). *Ramphotyphlops braminus,* with a nearly global distribution, has been collected from Hole-in-the-Donut and has been observed in Royal Palm Hammock since the early 1990s; however, the precise age of the colony and extent of its distribution in ENP remain unknown. *Python molurus bivittatus* has been reported from the saline glades and mangroves since the 1980s. Specimens were also collected on Main Park Road in 1996 and 1997. Unlike those collected from the south end of the park, individuals examined from Paradise Key appear to be recently released captives, based on their fat condition, absence of scars and parasites, and docile temperament.

Failed colonizations—A number of exotic species have appeared in ENP (Butterfield et al., 1997; Meshaka et al., 2000) but have apparently not become established as yet. These include *Bufo marinus, Anolis equestris, Ctenosaurus pectinata, Iguana iguana, Python reticulatus, Anolis distichus, Boa constrictor, Caiman crocodylus,* and *Python regius.* The latter four species are represented by single records, but the others have been sighted repeatedly. Exceptionally, *B. marinus* is ubiquitous in the agricultural fields adjoining ENP. We suggest that the seasonally xeric conditions of the Everglades could be the barrier to its establishment in ENP.

Threatened and endangered species—Seven species are federally listed (Table 1). With the exception of *Drymarchon corais couperi* and *Crocodylus acutus,* the remaining five federally listed species are marine turtles.

Marine species—Five marine species, all turtles, occur in ENP. *Dermochelys coriacea, Eretmochelys imbricata imbricata* and *Lepidochelys kempii* are uncommon within the park boundaries. However, the latter species was reported as common fifty years ago, and Florida Bay was considered its optimum habitat (Carr, 1952). *Chelonia mydas* is present in marine areas of ENP, most of which are sub-adults (Steiner and Bass, 1980). *Caretta caretta* is the most abundant species (Klukas, 1967; Davis and Whiting 1977) and is the only confirmed marine turtle that nests in the park. *C. caretta* nests after dark during the summer months on Cape Sable and the Florida Bay keys (Steiner and Bass, 1980).

Species of limited distribution in ENP—Six species appear to be genuinely restricted in distribution in ENP. Among the native species, *Sternotherus odoratus* and *Kinosternon subrubrum steindachneri* appear to be actually rare in ENP (Duellman and Schwartz, 1958; Dalrymple, 1988; specimens in ERCC). In other parts of their range, both species are often associated with permanent water. In this connection, *S. odoratus* is abundant in canals of extreme southern Florida (Duellman and Schwartz, 1958; Meshaka, 1989), and both species have been collected at the northern end of ENP in the Tamiami Canal (Duellman and Schwartz, 1958).

Gopherus polyphemus, established only on the sandy dunes of Cape Sable (Kushlan and Mazzotti, 1982), has the smallest distribution of turtles in ENP. Over the years, however, several individuals have been found on Long Pine Key. The origin of these individuals is unknown.

Among exotic species, all three geckos appear to be closely associated with buildings and disturbed areas (Meshaka, 1999; Meshaka et al., 1999). *Gekko gecko,* found only in Key Largo, is probably the most restricted of the geckos.

Species of questionable occurrence—At the level of subspecies, one amphibian and eight reptiles were collected from areas adjoining ENP, but not within the park itself by Duellman and Schwartz (1958) and do not appear to occur in ENP (Table 2). Although *Siren intermedia* has not been recorded from ENP (Duellman and Schwartz, 1958; Dalrymple, 1988; Machovina, 1994; ERCC), it was collected with *Siren lacertina* in an altered wetland farther north (Meshaka, 1997). *Siren lacertina* greatly outnumbers *S. intermedia* in collections made at the site (Meshaka, Unpubl. data). If *S. lacertina* also outnumbers *S. intermedia* in ENP, then the possibility remains that *S. intermedia* is present in the park, even if actually rare.

The occurrence in the park of five species of lizards and three species of snakes are questionable. *Ophisaurus attenuatus* and *Pituophis melanoleucus mugitus* were collected from Dade County (Duellman and Schwartz, 1958), and *Eumeces egregius egregius* and *O. ventralis* were collected in Dade and Monroe counties (Duellman and Schwartz, 1958). *Tantilla oolitica* and *Eumeces egregius onocrepis* were collected in southern Dade County and the upper Florida Keys (Duellman and Schwartz, 1958; Porras and Wilson, 1979; Telford, 1980). *Cnemidophorus sexlineatus sexlineatus* was also collected from the Upper Florida Keys (Duellman and Schwartz, 1958). *Sceloporus woodi* was collected from Miami by Duellman and Schwartz (1958) but has not since been recorded from Dade County. With the exception of *O. ventralis,* all questionable species of reptiles are associated with xeric upland habitats. If these species occur in ENP, the poorly studied sandy uplands of Cape Sable are the likeliest area for them to be found. The remaining species recorded by Duellman and Schwartz (1958) from southern Florida, exclusive of ENP (Table 2), either have geographic ranges that do not approach the park from the north or are exotic species with limited geographic ranges.

Temporal changes in species presence—Nine species of amphibians and reptiles, now recorded in the park, were either missed (N = 3) by Duellman and Schwartz (1958) or colonized the park subsequent to their study (N = 6). Two additional species were recorded from the park by Duellman and Schwartz (1958) that no longer appear to occur in the park, one of which may also no longer occur anywhere in extreme southern Florida. One species not recorded in the park by Duellman and Schwartz (1958) is represented by a single specimen but considered extirpated.

Of the three species apparently missed by Duellman and Schwartz (1958), *Osteopilus septentrionalis,* was released at Paradise Key in the park (Allen and Neill, 1953) several years prior to Duellman and Schwartz's (1958) study, but they failed to record it at that locality. Nonetheless, *O. septentrionalis* was probably in ENP at the time of their study, as Jones (1999) first saw the species in ENP in the early 1950s, and Bass (1999) observed *O. septentrionalis* as a common inhabitant of bathrooms on Long Pine Key and at Flamingo in the late 1950s. Establishment of this species in the park at some level during the late 1950s was followed with a boom of this species in nearby Homestead during the 1960s (Bass, 1999; Robertson, 1999). This coincided with a precipitous loss of native treefrogs in the urban landscape despite little significant change in the features of the local area (Bass, 1999; Robertson, 1999). These observations suggest that *O. septentrionalis* has probably been in the park at least since its release in the early 1950s and was firmly established, even if locally, by the end of the decade. The second species missed by Duellman and Schwartz (1958), *Gopherus polyphemus,* was earlier recorded from Cape Sable (Simpson, 1920; Simmons and Ogden, 1998), where it may have been introduced as a human food source. Three specimens of *Dermochelys coriacea* were collected at two sites in Dade County (Duellman and Schwartz, 1958). In light of its broad geographic range, limitations in sampling best explain absence of records from ENP.

Of those species apparently absent from ENP during the Duellman and Schwartz (1958) study, *Anolis sagrei* was in southern mainland Florida and the Florida Keys, but no voucher specimens or sight observations exist from within the park boundaries at that time. The history of colonization of *A. sagrei* in the park is unclear. Bass (1999) and Robertson (1999) recall the species in Homestead in the 1960s and in the park at least by the 1970s; however, neither is certain that they did not overlook the species prior to their first sightings of it in the park. Its history in Homestead, the conspicuous habits of this species, and the diligence of Duellman and Schwartz's (1958) searches, lead us to believe that *A. sagrei* was probably not in the park at the time of their study. If *A. sagrei* colonized the park after becoming established in Homestead, then only the timing of its subsequent colonization of the park, 1960s or 1970s, remains in question.

Gekko gecko has been established on the Upper Florida Keys at the Key Largo Ranger Station since at least the early 1990s, and colonies exist in the Homestead and Miami areas and sporadically throughout the Keys (Meshaka et al., 2000). *Hemidactylus garnotii* was in Dade County in the late 1950s or early 1960s (Wilson and Porras, 1983) and recorded in the park by Kluge and Eckhardt (1969). *Hemidactylus mabouia* was first captured in the park in 1990 (Butterfield et al., 1993) where it has since aggressively colonized buildings from Long Pine Key to Flamingo (Meshaka, 2000). *Ramphotyphlops braminus* has been reported repeatedly since the early 1990s. Park personnel have observed large pythons, some of which were identified as *Python molurus bivitattus,* since the 1980s. Everglades natural history record cards and specimens stored in the ERCC corroborate presence of various size-classes during the 1990s from the region between Paurotis Pond and the Buttonwood Canal, and is considered established (Meshaka et al., 2000).

Two species recorded by Duellman and Schwartz (1958) no longer appear to occur in ENP. *Scaphiopus holbrookii* has not been recorded from the park or from the general area (Dade, Broward, and Monroe counties), for more than forty years. Porter (1999) noted the decline of *S. holbrookii* in the south Miami-Coral Gables area of Dade County during the 1950s. Its extirpation in southern Florida is particularly noteworthy in light of historical abundance in the region. Because this form is a confirmed burrower across its geographic range and because the substrate suitable for burrowing is limited in ENP and extreme southern Florida, development of uplands and alteration of the hydroperiod best explain its demise. Since the 1950s, the dry season water tables have dropped precipitously concomitant with widespread hydrological changes in southern Florida (Parker et al., 1956; Loftus et al., 1992). We propose that because extremely low dry-season water tables became the norm as a result of water delivery changes in the 1960s, the previously abundant *S. holbrookii* would understandably have uniformly disappeared from the uplands of extreme southern Florida when dry season water was unavailable.

Heterodon platirhinos, whose geographic range historically extended into extreme southern Florida, was considered uncommon in the southern Everglades by Duellman and Schwartz (1958). They reported a single specimen on Cape Sable Road in ENP. This species is at least partly fossorial and mainly inhabits regions of sandy soil or oolitic limestone, such as found along the Atlantic Coastal Ridge, along parts of Florida Bay in the Cape Sable region, and on some Florida Bay keys. The increase in farming and urban development along the eastern edge of the park in the past forty years has resulted in the interruption of habitat connectance between the park and the coastal ridge, and potential source areas on the east coast are practically nonexistent, *H. platirhinos* probably no longer exists in ENP, and perhaps in extreme southern Florida generally.

Masticophis flagellum flagellum was collected in Dade and Broward counties by Duellman and Schwartz (1958) but not in the park where it is represented by a single specimen, a hatchling collected near Royal Palm Hammock in 1958. No other records of this otherwise largebodied and conspicuous species exist for the park. In light of these circumstances we propose that the park historically provided poor habitat for *M. f. flagellum* and, like *H. platirhinos*, isolation from and destruction of source areas best explain its extirpation from the park.

Taxonomic considerations—The taxonomic status of four polytypic species found in the park warrant consideration. Among the rat snakes, the two recognized forms in Florida, yellow rat snake (*Elaphe obsoleta quadrivittata*) and the Everglades rat snake (*E. o. rossalleni*), are both found in the park from Long Pine Key to Flamingo and Cape Sable; however, most individuals encountered possess morphological characteristics of both forms. The degree to which this represents a dilution of both forms on a greater geographic scale, particularly if mediated by humanity, remains an open question.

Among the thamnophines, three ribbon snakes are currently recognized that occur in Florida. The Eastern ribbon snake (*Thamnophis sauritus sauritus*) reaches no further south into Florida than the panhandle, where it is replaced by the bluestripe ribbon snake (*T. s. nitae*) in the Gulf Hammock region of the peninsula and by the peninsular ribbon snake (*T. s. sackeni*) in the rest of Florida. Ribbon snakes meeting the morphological criteria of each of the latter two forms have been collected along the Main Park Road from Long Pine Key to Flamingo. The presence of both forms and a majority of intergrades (e.g. a blue belly and complete tan dorsal stripe) in the southern Everglades gives cause to warrant re-evaluation of the status of *T. s. nitae* with respect to its geographic range and its validity as a subspecies.

A similar situation exists in the garter snakes found in ENP. Fresh and preserved garter snakes examined from the region of Long Pine Key to Flamingo consistently are found with an overall bluish ground color, deep blue belly, and distinct tan dorsal stripe. The lateral stripe is weakly defined, but also blue in color. Animals are dorso-laterally checkered in black. This description is more similar to that of the bluestripe garter snake (*Thamnophis sirtalis similis*) of the Gulf Hammock region of Florida than it is to the eastern garter snake (*T. s. sirtalis*). As in the case of the ribbon snake, why a bluish form predominates in a region distant from its known range remains an interesting taxonomic question.

A Gulf Hammock-extreme southern Florida connection in the morphology of herpetofaunal elements also exists with the striped mud turtle (*Kinosternon baurii*). The poorly defined (if even present) carapace stripes, a defining characteristic of the Florida keys populations (*K. bauri bauri*), was also observed in Gulf Hammock populations (*K. b. palmarum*) and provided an argument to reject the validity of the keys subspecies (Iverson, 1978b). Indistinct, if any, striping on the carapace of ENP *K. baurii,* like those of the keys and Gulf Hammock, further supports Iverson's (1978b) conclusions.

Lastly, the taxonomic status of the leopard frog in Florida remains in question. At least one form, the southern leopard frog (*R. sphenocephala*), is recognized as a species distinct from the northern leopard frog (*R. pipiens*) and occurs throughout Florida. As a polytypic species, the southern leopard frog (*Rana sphenocephala utricularia*) geographically ranges southward to northern Florida and is replaced southward by the Florida leopard frog (*R. s. sphenocephala*). Validity of this polytypic arrangement remains equivocal, and until further evidence supports that arrangement we identify the leopard frogs of ENP as *R. sphenocephala.*

Habitat associations—Based on 16 habitats recognized for this inventory from the literature, field work in ENP, and collections of the ERCC (Table 1), most species have been recorded in more than one habitat. The rest of the ENP herpetofauna is evenly distributed between wetlands, uplands, or both. Four of the exotic species are established in natural habitats. Only *Pseudacris nigrita verrucosa* and *Ophisaurus compressus* are strongly transitional species with respect to habitat, occurring nearly exclusively along the interface of uplands and prairies. The three hylid treefrogs were recorded from the highest number of habitats. The highest number of species were recorded from marshes, pinelands, and tropical hardwood hammocks.

Predictions of future changes in the ENP herpetofauna—Since the study of Duellman and Schwartz (1958), three species (*Scaphiopus holbrookii, Heterodon platirhinos*, and *Masticophis flagellum flagellum*) have been lost, and six exotic species (*Anolis sagrei, Gekko gecko, Hemidactylus garnotii, Hemidactylus mabouia, Python molurus bivittatus, Ramphotyphlops braminus*) have become established in ENP. Based upon changes outside of ENP and proposed changes within ENP, we predict two unrelated trends for the ENP herpetofauna.

Our first prediction relates to the proposed hydrological restoration of ENP that will divert more water through the park during the wet season and maintain much higher dry-season water tables than in the past 40 years. Because of the mostly generalized habits of the park's herpetofauna, faunal changes are more likely to be expressed in relative abundance rather than in actual presence/absence of species. For example, with longer hydroperiods and more accessible water during the dry season, we expect to see higher abundances of aquatic species such as the four salamanders, *Rana grylio, Acris gryllus dorsalis,* and *Alligator mississippiensis.* In the case of *A. mississippiensis,* we expect that its population will increase in the peripheral marshes on both sides of Shark Slough, the opposite of the present situation.

Our second prediction relates to exotic-species invasions. Because the park adjoins a highly urbanized region which has the highest number of exotic species of amphibians and reptiles in Florida (Meshaka et al., 2000), we expect increased appearances of exotic species that will exceed past rates. This will result from the continual influx of exotic species into Florida, and because of constant human traffic into the park. Based on the trends of the exotic herpetofauna in southern Florida (Meshaka et al., 2000), more geckos associated with buildings will precede the invasions of other species. The next exotic species to enter ENP is likely to be *Basiliscus vittatus,* which occurs along canals in Dade County. For the same reasons, we think that *Iguana iguana* and *Ctenosaurus pectinata* will become more prevalent in ENP.

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A NEW RECORD FOR *SCHISTOCERCA CERATIOLA* (ORTHOPTERA: ACRIDIDAE)

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ABSTRACT: Schistocerca ceratiola *Hubbell and Walker, the rosemary grasshopper, was collected from a* Ceratiola ericoides *Michx plant community on a sand ridge in Levy County, northern Florida where its presence has been suspected for many years. The grasshopper's behavior and distribution on the unique ridges of the Florida peninsula are discussed.*

THE ROSEMARY grasshopper, *Schistocerca ceratiola,* an elusive and seldom encountered grasshopper as compared to other *Schistocerca* species, has now been recorded in Levy County, Florida.

Schistocerca ceratiola is one of the 17 known grasshoppers that are precinctive to Florida (Capinera et al., 2000). The rosemary grasshopper is restricted to scrub and sandhill habitats on Florida ridges. These ridges were islands around 25 million years ago (Myers, 1990). To some arthropods these areas are still "islands" today because they are restricted to this habitat by their dependence on food plants or the actual physical environment (Deyrup, 1989). Insect physical characteristics such as reduced wings and actual environmental barriers such as wetlands also play a role in maintaining these island-like communities. The rosemary grasshopper is found on these ridges due to the availability of its host plant, Florida rosemary, *Ceratiola ericoides* Michx. *Schistocerca ceratiola* seems to be monophagous (Deyrup and Franz, 1994), an uncommon trait as most grasshoppers are polyphagous or oligophagous (Chapman and Joern, 1990). Hubbell and Walker (1928) believed that the characteristics of slender form, cryptic coloration, hesitance to fly, and nocturnal habits resulted from monophagous feeding on rosemary. Florida rosemary is a perennial shrub in the family Empetraceae. Plants reach heights from 3 to 5 meters (Hall, 1993). The range of *Ceratiola ericoides* is from Florida to South Carolina and as far west as Mississippi (Hall, 1993). *Schistocerca ceratiola* does not appear to occur throughout the range of its host plant. A possible reason for this could be that in the northern ranges the host plant occurs in habitats other than sandhill and scrub ridge habitats. *Schistocerca ceratiola* may require not only the presence of the host plant but also the specific environment (architecture) that sandhill and scrub habitats offer.

At the time of discovery of *Schistocerca ceratiola* (Hubbell and Walker,

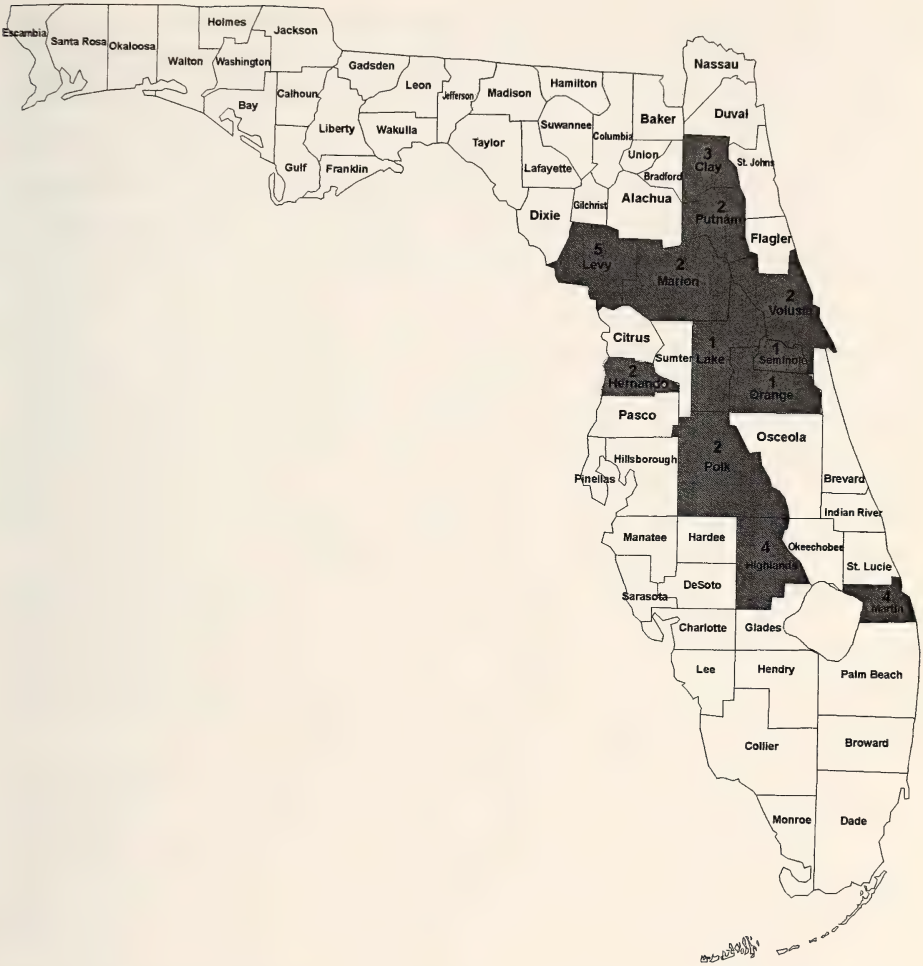

FIG. 1. Chronological distribution of *Schistocerca ceratiola* throughout Florida counties. 1. Hubbell and Walker, 1928. 2. Dirsh, 1974. 3. Franz and Franz, 1989. 4. Deyrup, 1989. 5. Squitier, 1997.

1928), the established range was believed to be restricted to 3 counties in central Florida: Orange, Seminole, and Lake (Fig.1). Dirsh (1974) extended the known range north and west into Hernando, Marion, Polk, Putnam, and Volusia counties. Franz and Franz (1989) extended the grasshopper's range to the northeast with the addition of Clay county. Deyrup (1989) indicated that this species occurs in Martin and Highlands counties, locations that expanded the range southward. The most recent record of *Schistocerca ceratiola* is in Levy county. The site is on the North Brooksville Ridge 6 km west of the town of Archer along State Road 24. The collection date was 4 September 1997. Previous collecting attempts by Hubbell and Walker in the 1920s and Franz and Franz in the 1980s at rosemary habitat near Archer were unsuccessful (Franz and Franz, 1989). Could *Schistocerca ceratiola's* concealing ability be perfected to the degree that it could evade being collected in this location for 70 years leading to its disjunct distribution records which Deyrup (1990) states is common for specialized ridge inhabitants?

Schistocerca ceratiola is infrequently encountered, partly because it has such a restricted host range. Additionally, these grasshoppers are rarely encountered since, instead of flying when disturbed, they cling motionless to the interior branches of the rosemary (Hubbell and Walker, 1928). This behavior is very unusual among *Schistocerca spp. Schistocerca* species such as *S. americana, S. damnifica,* and *S. alutacea* will fly great distances when disturbed. The branches of the rosemary match the mottled brown and greenish coloration of the grasshopper making it very hard to detect. Hubbell and Walker (1928) state that they collected an entire afternoon only to capture 1 or 2 specimens but upon returning to the same foliage that night found many specimens feeding and copulating on the outer foliage. Dirsh (1974) cited nocturnal activity and narrow habitat range as reasons why *Schistocerca ceratiola* was not discovered until the 1920s.

This recent collection in Levy county adds the North Brooksville Ridge to the known distribution by ridges of *Schistocerca ceratiola* as described by Deyrup (1990). Florida's ridges do not run continuous through adjoining counties nor are the ridges contiguous with one another. Would it be possible for *Schistocerca ceratiola* to migrate to unpopulated rosemary communities separated by great distances of unfavorable habitat?

Deyrup and Franz (1994) include *Schistocerca ceratiola* in their list of rare and endangered biota of Florida. The grasshopper simply does not have much habitat remaining to inhabit. Kautz et al. (1993) states that the declining acreage of scrub and sandhill habitats, an 88% loss for sandhill and a 59% loss for scrub habitat since settlement, is a matter of interest due to the large number of rare and endemic species found only in these habitats. The Levy county site is not a safe haven for the grasshopper for it is currently under development. However there are protected preserves of sandhill and scrub habitat in Highlands, Martin, Marion, Polk and Putnam counties. If time will allow, further research needs to be carried out on these interesting relic grasshoppers. With each new collection of the rosemary grasshopper Hubbell's question of will *Schistocerca ceratiola* be found throughout *Ceratiola ericoides'* range is closer to being answered.

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Biological Sciences

A COMPARISON OF SCRUB HERPETOFAUNA ON TWO CENTRAL FLORIDA SAND RIDGES

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ABSTRACT: *Florida scrub is one of the most threatened ecosystems in Florida. There is urgent need for basic research directed toward scrub species if their needs are to be considered in conservation planning. We report the results of a herpetological survey conducted in scrub on Avon Park Air Force Range (APAFR) and the Arbuckle Tract (AT) of the Lake Wales State Forest from May 1994–October 1998 using visual surveys, trap arrays, trapping grids, and coverboards. These two areas of scrub are located on ridges of different geologic origin (APAFR, Bombing Range Ridge; AT, Lake Wales Ridge). Forty species were captured on APAFR, and 15 species on AT, where survey intensity was lower. The most commonly trapped reptiles (*Anolis carolinensis, Cnemidophorus s. sexlineatus, Sceloporus woodi, *and* Tantilla relicta neilli*) were captured throughout the year with the lowest rates of capture occurring during the coldest months (December–January). Captures of amphibians were more seasonal, and included adults moving through scrub to breeding ponds and metamorphs dispersing from ponds. Data on movements of recently metamorphosed gopher frogs (*Rana capito aesopus*) indicate that peak reproductive activity of this species occurs in winter, as reported for northern populations. Although the herpetofauna in APAFR scrub is generally similar to the fauna reported for the Lake Wales Ridge, the sand skink (*Neoseps reynoldsi*) and the bluetail mole skink (*Eumeces egregius lividus*) were not recorded on APAFR despite intensive sampling. Both species were captured on the Arbuckle Tract. These data are consistent with other reports that suggest the two skinks are not found on the Bombing Range Ridge.*

FLORIDA scrub, and its endemic fauna, is one of the most threatened ecosystems in Florida (Millsap et al., 1990). Scrub occurs on sandy, well-drained soils on relict sand dunes of the central ridge of the Florida peninsula and in strands along more recent coastal sand dunes (Christman, 1988; Fernald, 1989; Myers, 1990). This unique system is naturally fragmented into an archipelago of habitat islands surrounded by more mesic and hydric habitats unsuitable for obligate scrub organisms. In the last several decades, the number and size of scrub patches have diminished and the isolation of patches has increased as a result of conversion of scrub to citrus groves and increasing urbanization. Although Florida scrub is the focus of major conservation initiatives at the state and national levels (USFWS, 1991), the dynamics of this system are poorly understood and only a few scrub species have been studied in detail.

This paper reports the results of a herpetological survey in scrub on

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Avon Park Air Force Range (APAFR), Polk and Highlands counties, and on the Arbuckle Tract (AT) of the Lake Wales State Forest, Polk County. APAFR and AT contain two of the largest areas of scrub in central Florida (approximately 2300 ha and 1020 ha, respectively). This work was conducted in conjunction with a landscape-level study of the Florida scrub lizard (Hokit et al., 1999). In addition to the scrub lizard, three other species were of special interest: the bluetail mole skink (*E. egregius lividus*), the sand skink (*N. reynoldsi*), and the Florida gopher frog (*R. capito aesopus*). The two skinks are listed as threatened species at the state and federal levels, and the gopher frog is a Species of Special Concern (Wood, 1996). Both skinks occur on the Lake Wales Ridge in central Florida, but neither has been recorded from the neighboring Bombing Range Ridge, which bisects APAFR. The natural history of the gopher frog is not well known in southern Florida (Altig and Lohoefener, 1983; Bailey, 1990; Semlitsch et al., 1995; Palis 1998). Some sources report the presence of a dwarf race of the Florida gopher frog on the Lake Wales Ridge in Polk and Highlands counties (Lee, 1973; Conant and Collins, 1991). Lee (1973) described this southern race as being ecologically isolated and bounded by the Peace River on the west, the Kissimmee River on the east, the Green Swamp on the north, and the Everglades on the south. APAFR is located within the area described by Lee (1973).

STUDY AREA—Our study was conducted throughout the scrub on Avon Park Air Force Range (15 km east of Avon Park, Florida) and the Arbuckle Tract of the Lake Wales State Forest (12 km east of Avon Park). Scrub has been defined in a variety of ways, and in our survey included xeric upland habitats commonly called sand pine (*Pinus clausa*) scrub, oak scrub, rosemary (*Ceratiola ericoides*) scrub, or scrubby flatwoods (Myers, 1990). We also surveyed the small amount of sandhill habitat (21 ha) present on APAFR. Scrub habitat on APAFR and AT is distributed patchily within an extensive matrix consisting predominantly of flatwoods, wet and dry prairies, marsh, and cypress swamps. Unlike many other areas where scrub patches are the result of recent fragmentation, scrub on APAFR and AT is naturally patchy. Aerial photographs spanning 6 decades indicate that the configuration of these patches has not changed, even though habitat quality has varied.

Although separated in places by as little as 2 km, the scrub patches on APAFR and AT are distinct in their geomorphic origins (White, 1970; The Nature Conservancy, 1994). Most scrub on APAFR is associated with the Bombing Range Ridge that rises from the Osceola Plain and is thought to be a relict marine sand bar. The Arbuckle Tract is considered part of the Lake Wales Ridge, a large relict sand dune deposit extending through the middle of Polk and Highlands counties. The Arbuckle drainage, including Arbuckle Creek, Arbuckle Lake, and Blue Jordan Swamp, separates the two upland areas.

METHODS—*Mapping scrub patches*—We visually delineated all scrub patches on APAFR and the Arbuckle Tract from soil, topographic, and vegetation maps and infrared aerial photographs. Because scrub communities are adapted to elevated, well-drained, sandy soils, scrub patches generally can be distinguished easily from the surrounding matrix in aerial photographs. Boundaries of patches were drawn on aerial photographs and digitized on scanned infrared aerial images. Ninety-five scrub patches, comprising over 2300 ha of scrub habitat, were mapped on APAFR. We delineated 37 scrub patches (total 1020 ha) on the Arbuckle Tract.

Patch surveys—From 1994–1998, we visually surveyed 67 to 95 scrub patches annually on APAFR. All patches on the Arbuckle Tract were surveyed at least once between September 1995 and March 1996. The primary goal of these surveys was to determine the presence/absence of scrub lizards, bluetail mole skinks, and sand skinks in each scrub patch. However, all herpetofaunal species that were encountered during searches were noted. Surveys involved visually searching for scrub lizards and sand skink tracks, and raking for sand skinks and bluetail mole skinks under palmetto fronds, aprons of sand at gopher tortoise (*Gopherus polyphemus*) burrows, and under other debris likely to be microhabitat for skinks. We surveyed patches from March–October and occasionally on warm afternoons from November–February. Patches in which no scrub lizards were found on the first attempt were surveyed more often (2–5 times each year). Large patches (>20 ha) were surveyed in 10 to 20-ha sections. Each patch or section was searched by two persons for a minimum of 30 min in 1994, and in subsequent years, for 30 min or until a scrub lizard was observed.

Herpetological trap arrays—We established 12 herpetological trap arrays in May 1994 following the techniques used by Campbell and Christman (1982) and Mushinsky and McCoy (1991). Each trap array consisted of four drift fences of aluminum flashing (7.5-m long by 36-cm wide) arranged in a cross with a gap of 3 m in the center. We sank pitfall traps (eight 20-liter plastic buckets per array) into the ground at the ends of the flashing. Our trap arrays differed from previous studies in that we did not use funnel traps along the drift fences because we were primarily concerned with capturing fossorial skinks.

The 12 arrays were located in 9 scrub patches on APAFR from May to December 1994. In January 1995, one array was moved to a patch of turkey oak (*Quercus laevis*) on APAFR and two arrays were relocated to scrub patches on the Arbuckle Tract. Pitfall traps associated with arrays were opened for one-week periods, once each month, from May 1994–April 1995 (total trap nights = 3496). When open, we checked traps daily and measured, marked, and released all amphibians and reptiles that were captured.

Coverboards—In 1995, we established coverboard grids in 10 scrub patches on APAFR and in two scrub patches on the Arbuckle Tract. Masonite coverboards (6-mm thickness, each 130 cm by 60 cm) were spaced at 20-m intervals in a 3 × 4 grid with one grid per patch. Once a week from January–April 1995, we turned over each coverboard and raked through the underlying substrate. In November 1995, the 120 coverboards from scrub patches on APAFR were relocated to two small patches of sandhill habitat dominated by turkey oak in order to intensively sample these areas for mole skinks. We checked the coverboards in these new locations and on Arbuckle Tract once a week from December 1995–May 1996 and biweekly in June and July 1997.

Trapping grids—Eight trapping grids, each one hectare in size, were installed in eight scrub patches on APAFR. Each grid consisted of 100 pitfall traps (20-liter plastic buckets) spaced at 10-m intervals. Six grids were trapped from January 1995–July 1996, and two additional grids were trapped from May 1995–July 1996. In 1997, the eight grids were trapped from June–July. Traps were opened for one week each month (total trap nights = 62,400). We checked traps daily and marked and released all amphibians and reptiles that were captured. Snout-vent length (SVL) also was measured for gopher frogs and scrub lizards. In addition, amphibians and reptiles observed on the grids, but not captured in bucket traps, were caught by hand and marked and released.

RESULTS AND DISCUSSION—*General survey results*—Our study documented 40 species of reptiles and amphibians in scrub habitat on APAFR (Table 1). One species listed (Wood, 1996) as Threatened (eastern indigo snake, *Drymarchon corais couperi*) and two Species of Special Concern (the gopher tortoise and gopher frog) were commonly found in scrub. We also captured one Florida pine snake (*Pituophis melanoleucus mugitus*), which is listed as a Species of Special Concern (Wood, 1996). Because of the lower survey effort, we documented only 15 species of amphibians and reptiles on the Arbuckle Tract (Table 1), all of which also were found on APAFR except the sand skink and bluetail mole skink.

Three species of lizards (*A. carolinensis, C. s. sexlineatus, S. woodi*) and the Florida crowned snake (*T. relicta neilli*) were the reptiles most commonly captured on the trapping grids (Table 1). These species were captured throughout the year (Table 2), except no *C. s. sexlineatus* and *T. relicta neilli* were trapped in December and January when temperatures reached peak lows (mean daily temperature for December–January = 10°C). Capture rates for *A. carolinensis, T. relicta neilli,* and, to a certain extent, *S. woodi* were lower during the wettest months of the year (June–September). Captures of most species of amphibians were more seasonal and associated with dispersal of metamorphs and movement of adults through scrub to breeding ponds in the matrix around scrub (Table 2). For example, 85 *Rana catesbieana* were captured on a single rainy night in one grid in November. Captures of *Bufo terrestris, Gastrophryne carolinensis,* and *Rana sphenocephala* primarily occurred in the wetter summer months (May–August). Captures of *Bufo quercicus* and *R. capito* (see below for details on gopher frogs) peaked during this period also, but numerous captures also occurred during other months (Table 2).

Gopher frogs—Florida gopher frogs (n = 301 individuals) were caught in 13 scrub patches on APAFR during this study. The smallest male with discernible vocal sacs was 61-mm SVL. We categorized all frogs 61 ≥ mm SVL, as adults. Adult frogs were captured infrequently ($\leq$4/month), but in every month except November. Our data do not indicate that gopher frogs on APAFR are part of a dwarf race. The body size of adults ranged from 61–92 mm SVL (mean = 73 mm ± 8) for 11 males and from 65–96 mm SVL (mean = 77 mm ± 7) for 13 females. These body sizes are comparable to those found in northern populations of gopher frogs (Lee, 1973; Franz, 1986; Bailey, 1990; Semlitsch et al., 1995). Nine of the 13 females and five of the 11 males were larger than the largest gopher frog captured by Lee (1973) in the Lake Wales Ridge region. We emphasize that all our captures were made on APAFR. Although located within the area delineated by Lee (1973), the xeric upland habitat on the Bombing Range Ridge is not con-

TABLE 1. Amphibians and reptiles captured or observed in patch surveys on Avon Park Air Force Range and the Arbuckle Tract.[1] Numbers in parentheses are for the Arbuckle Tract. Y = observed in patch survey.

Species	Trapping Grids	Trap Arrays	Cover-boards	Patch Surveys
AMPHIBIANS				
Acris gryllus dorsalis	22	4		
Bufo quercicus	517	238 (3)		Y (Y)
Bufo terrestris	62	18 (3)	1	Y
Eleutherodactylus planirostris	32	8		
Gastrophryne carolinensis	75	75 (2)		
Hyla cinerea	1			
Hyla femoralis	46	9	5	Y
Hyla gratiosa	3	1		
Hyla squirella	2	2		
Rana capito aesopus	245	66		Y
Rana catesbeiana[2]	104	2		
Rana grylio[2]	7			
Rana sphenocephala	86	6		Y
REPTILES				
Anolis carolinensis	264	12	125 (1)	Y (Y)
Apalone ferox				Y
Cemophora c. coccinea	24			
Cnemidophorus s. sexlineatus	306	85 (2)	25 (1)	Y (Y)
Coluber constrictor priapus	22	5	15	Y (Y)
Crotalus adamanteus	1			Y
Drymarchon corais couperi	8			Y (Y)
Elaphe g. guttata			1	
Elaphe obsoleta quadrivittata	1			Y
Eumeces egregius lividus			(2)	
Eumeces inexpectatus	23	9	19	Y (Y)
Gopherus polyphemus	4	2		Y (Y)
Heterodon platirhinos	1			
Lampropeltis triangulum elapsoides	1	1		
Masticophis f. flagellum	11	(1)	2 (1)	Y (Y)
Micrurus f. fulvius	2			
Neoseps reynoldsi		(6)	(2)	(Y)
Opheodrys aestivus	1			Y
Pituophis melanoleucus mugitus	1			
Regina alleni	1			
Rhineura floridana				Y
Scincella lateralis	6	9		Y
Sistrurus miliarius barbouri				Y
Sceloporus woodi	1630	124 (8)	68 (3)	Y
Storeria dekayi victa	1			
Tantilla relicta neilli	64	2 (4)		
Terrapene carolina bauri	1			Y
Thamnophis sauritus sackenii	1	(1)		Y
Thamnophis s. sirtalis		1		Y

[1] Numbers given for trap arrays and trapping grids represent counts of unique individuals. The number of individuals listed for coverboards represents the number of captures, including recaptures (see text).

[2] The total number for each species represents our "best guess" at discriminating between young bullfrogs and pig frogs.

TABLE 2. Number of individuals captured in each month on trapping grids for species with over 50 captures at Avon Park Air Force Range.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
AMPHIBIANS												
Bufo quercicus	0	4	6	35	203	206	91	47	11	4	7	0
Bufo terrestris	0	0	0	8	35	24	11	5	2	1	0	3
Gastrophryne carolinensis	1	0	0	0	7	32	17	23	2	3	3	1
Rana capito	7	3	5	46	116	41	42	12	2	17	9	3
Rana catesbeiana	0	0	2	0	6	4	3	0	0	21	85	1
Rana utricularia	0	0	0	1	51	18	26	0	0	1	1	0
REPTILES												
Anolis carolinensis	1	28	75	38	28	19	16	27	6	7	19	29
Cnemidophorus s. sexlineatus	0	1	40	51	47	37	119	50	18	14	2	0
Sceloporus woodi	193	400	515	485	488	539	479	531	536	397	361	236
Tantilla relicta neilli	0	5	15	8	12	10	5	2	4	3	8	0

tiguous with the Lake Wales Ridge system (USFWS, 1991). A dwarf race may exist on the Lake Wales Ridge proper.

Northern populations of gopher frogs (e.g., Alabama, South Carolina, and northern Florida) typically breed between January and April (Franz, 1986; Bailey, 1990; Godley, 1992; Semlitsch et al., 1995; Palis, 1998). Populations in central and southern Florida are thought to breed primarily between May and July in association with the rainy season (Godley, 1992). However, Enge (in press) reported large numbers of gopher frogs moving to breeding ponds in October in Hernando County. In our study, recently metamorphosed juveniles of the gopher frog (individuals 33–40 mm SVL) were captured in every month except January–March and the month of September. Thus, young appear to emerge in two periods: April–August and October–December. Most metamorphs were captured in April–July. If larval development takes 3–4 months (Godley, 1992; Semlitsch et al., 1995), oviposition for these metamorphs probably occurred in January–March. Also, a large number of individuals 40–45 mm in size were captured in April, May, and June. If the growth rate of recently metamorphosed frogs is 1.5–2.5 mm per month (Bailey, 1990; Godley, 1992), oviposition for these 40–45-mm frogs probably occurred in November or December. These larger froglets may stay in or near pond sites until the rainy season allows for more successful dispersal.

Our data suggest that most APAFR gopher frogs breed in rough synchrony with northern populations. The most successful reproductive activity of gopher frogs on APAFR occurs during the winter months from November–March even though rainfall is relatively sparse during this period. The cohort of metamorphs captured from October–December indicates that some breeding occurs during the rainy season in summer. Our conclusions concerning the reproductive chronology of northern and southern populations of gopher frogs depend upon two key assumptions derived from studies of northern populations: 1) the larval developmental period is 3 to 4 months, and 2) the growth rate of newly metamorphosed individuals is 1.5 to 2.5 mm per month. Careful study of southern populations may not support these assumptions. Furthermore, our conclusions are based on data from one isolated ridge of upland xeric habitat. Life history traits may vary among such geographically isolated units.

Distribution of the endemic scrub lizards—The Florida scrub lizard occurred in only 29 of the 95 scrub patches on APAFR and in 17 of the 37 scrub patches on the Arbuckle Tract. Their distribution is strongly influenced by the amount of open sandy habitat, patch size, and patch isolation (Hokit et al., 1999). Patches that were more than 750 m from a patch occupied by scrub lizards did not have scrub lizards, even when habitat was appropriate (Hokit et al., 1999). Despite our intensive surveys, the sand skink and bluetail mole skink were not found on APAFR. Conversely, with relatively little effort we captured eight sand skinks and two bluetail mole skinks on the Arbuckle Tract. Also, brief visits to other areas on the Lake Wales Ridge resulted in the capture of 15 sand skinks and five bluetail mole skinks (Hokit, pers. obs.). Given the high visibility of sand skink tracks and the relatively easy capture of specimens on the Lake Wales Ridge, it is unlikely that we missed this species if it occurs on APAFR. Some sources restrict the distribution of the sand skink to the Lake Wales Ridge, Winter Haven Ridge, and Mount Dora Ridge (Christman, 1992a). Similarly, the bluetail mole skink is considered restricted to the Lake Wales Ridge (Christman, 1992b), although the closely related peninsula mole skink (*Eumeces egregius onocrepis*) is more ubiquitously distributed and found in habitat types that are present on APAFR (Ashton and Ashton, 1991). We did not document any subspecies of the mole skink on APAFR.

Comparisons with other studies—Overall, the herpetofauna in scrub habitat on APAFR compares well with areas on the Lake Wales Ridge. Mushinsky and McCoy (1991) captured 36 herpetological species in their study of 16 scrub patches on the Lake Wales Ridge. In our scrub surveys, we captured or observed all but five of the species observed in their study; the sand skink, bluetail mole skink, eastern spadefoot toad (*Scaphiopus holbrookii*), eastern glass lizard (*Ophisaurus ventralis*), and black swamp snake (*Seminatrix pygaea*) were not observed in scrub habitat on APAFR. The black swamp snake is not considered a characteristic scrub vertebrate (Christman, 1988) and we have observed this species in hydric and mesic habitats on APAFR. Other herpetofaunal species sometimes captured in scrub habitat on the Lake Wales Ridge (Christman, 1988) that were not documented in our scrub study included the eastern slender glass lizard (*Ophisaurus attenuatus longicaudus*), southern ringneck snake (*Diadophis *p. punctatus*), and the short-tailed snake (*Stilosoma extenuatum*). The slender glass lizard and southern ringneck snake may not be common in scrub habitat (Mushinsky and McCoy, 1991) and, although we did not capture either species in scrub patches, we have observed both in other habitats on APAFR. The short-tailed snake is considered rare and secretive (Campbell, 1992) and may be difficult to document.

We captured or observed nine herpetofaunal species not recorded in Mushinsky and McCoy's (1991) scrub study: the bullfrog, pig frog (*Rana grylio*), eastern diamondback rattlesnake (*Crotalus adamanteus*), eastern coral snake (*Micrurus f. fulvius*), rough green snake (*Opheodrys aestivus*), striped crayfish snake (*Regina alleni*), dusky pigmy rattlesnake (*Sistrurus miliarius barbouri*), Florida box turtle (*Terrapene carolina bauri*), and peninsula ribbon snake (*Thamnophis sauritus sakenii*) were all found at least once in scrub habitat on APAFR. Four of these species (the eastern diamondback rattlesnake, eastern coral snake, rough green snake, and dusky pigmy rattlesnake) are considered characteristic scrub vertebrates (Christman, 1988).

Some species may have been missed in our surveys because of their low population densities or because they occur in locations that were under represented in our surveys. In addition, snakes may be under represented because of the lack of funnel traps associated with trap arrays. Alternatively, some species, such as the sand skink and bluetail mole skink, may be absent from APAFR because of dispersal and/or habitat constraints. Several species of plants that are endemic to scrub habitat on the south Lake Wales Ridge are not found on APAFR, a pattern that may result from the unique geomorphology of the Bombing Range Ridge (Orzell, 1993). The Arbuckle drainage system that separates the Bombing Range Ridge from the Lake Wales Ridge may be an effective dispersal barrier for some herpetofaunal species. Genetic studies indicate that scrub lizard populations on APAFR and the Arbuckle Tract share only one of 11 mtDNA haplotypes, suggesting that dispersal of scrub lizards is restricted between these areas but has occurred at some time in the past (Clark et al., 1999). The relatively patchy mosaic of habitat types on APAFR also may create landscape conditions unsuitable for the long-term persistence of some scrub organisms. For example, the spatial configuration of the landscape strongly influences the persistence of the Florida scrub lizard (Hokit et al., 1999).

Our survey demonstrates similarities and differences in species composition between two sand ridges in close proximity. Detailed distribution information is available for only a few scrub species (Stith et al., 1996; Branch et al., 1999), even though such data are important for conservation planning. For example, our data indicate that APAFR provides habitat protection for the Florida scrub lizard, but not the sand skink and the bluetail mole skink. Management of this area is important for conservation of the Florida scrub lizard because of the large amount of scrub habitat and because lizard populations on the Bombing Range Ridge harbor unique genetic diversity not found in populations on other reserves (Clark et al., 1999). Ecological studies of scrub species with a diversity of life history traits, as well as more detailed distribution data, are needed as a basis for managing this increasingly rare ecological system.

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USE OF A COMPUTER-INTERFACED SYSTEM FOR DETERMINATION OF THE INHIBITION OF OXYGEN PRODUCTION BY SELECTED AQUATIC WEEDS IN THE PRESENCE OF CATTAIL (*TYPHA DOMINGENSIS*) EXTRACTS

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ABSTRACT: *The phytotoxicity of aqueous extracts of cattail (*Typha domingensis*) towards selected aquatic weeds was studied through the short-term impact of exposure to cattail extracts on the rates of oxygen production by the weeds. Rates were quantified using a dissolved oxygen sensor and a computer-interface system (LabworksII). We determined the average dissolved oxygen concentrations before and after addition of the known amounts of extracts. Results indicate that cattail extracts (610 ppm Corg) inhibit the oxygen production of three of the five plants studied (*Vallisneria spp., Elodea canadensis, *and* Myriophyllum spp.*).* Cabomba caroliniana *showed only slight inhibition, and* Hydrilla verticillata *(Royle) was unaffected.*

INVASIVE non-native freshwater plants are competing with Florida's native species for space, nutrients and sunlight, and they can disrupt the ecosystem (Pieterse and Murphy, 1990). Aquatic plants that grow completely or mostly under water are often termed "oxygenating" or "oxygen" plants for their contribution of dissolved oxygen during photosynthesis. Admittedly, dissolved oxygen is important to support fish and other aquatic life. These plants also provide food and cover for fish and other aquatic organisms. However, such exotic plants as *Hydrilla verticillata* (Royle) have the potential to multiply at an increased rate, becoming problematic. Terming this plant "oxygen grass" does not mitigate its harmful effects, as the invasion of the Potomac River must surely demonstrate (Steward et al., 1984)

We selected five plants that are considered to be nuisance species in different regions of the United States (Hoyer, 1997). Fanwort or Cabomba (*Cabomba caroliniana*) is a noxious weed in the Northwest. Water celery or tape grass (*Vallisneria americana*) is found in freshwater and is being replaced by other aquatic weeds. Eurasian watermilfoil (*Myriophyllum spp.*) is possibly the worst aquatic weed in the northern United States and Canada. Hydrilla (*Hydrilla verticillata* Royle) is an exotic, rootable, submersed perennial aquatic plant that is causing serious hindrance in the southeastern United States (Barltrop et al., 1984; Langeland, 1996), and elodea (*Elodea *canadensis*) has caused critical problems in Central Florida (Burkhalter et al., 1973).

Previous research dealing with aqueous extracts of *T. domingensis* has noted the phytotoxicity (Prindle and Martin, 1996). Aqueous extracts inhibited the germination of lettuce and radish seeds and reduced oxygen production rates of the cyanobacterium *Lyngbya majuscula*; the aqueous extracts were found to be active even after being autoclaved. When these extracts were studied using gas chromatography-mass spectrometry, two of the major components of the extracts were found to be 2-chlorophenol and salicylaldehyde (Prindle et al., 1997). The relative concentrations of these compounds in the extracts have been determined and were found to be on the order of mg per kg of fresh material (Gallardo et al., 1999). These compounds have been detected in sediments in the *T. domingensis* growth front but not in sediments 2 m away from the cattail infestation (Albalat et al., 1997). Cattail extracts were also inhibitory towards the growth and propagation of *Salvinia minima* (Gallardo et al., 1998) and could decrease its oxygen production (Gallardo et al., 1999).

The purpose of this research was to determine whether cattail extracts could inhibit the selected aquatic weeds. In order to do so, we used a dissolved oxygen probe to monitor the dissolved oxygen concentration in the microenvironment that contained the selected weed before and after addition of cattail extract. The results obtained in this short-term bioassay could be used as an indication of the inhibitory potential of the cattail materials against a particular weed.

MATERIALS AND METHODS—*Culturing of plants*—Aquatic plants were obtained from Carolina Biological Supply (Burlington, NC) and cultured in Hoagland's medium (Steward and Elliston, 1973) and then placed under cool-white fluorescent tubes for 7–10 days. This was done to allow for initial growth of the plants.

Preparation of cattail extracts—Fully mature samples were taken from a storm water ditch near the University of South Florida campus in Tampa, Florida. Samples were identified and, after collection, were rinsed with deionized water and divided into three sections: root system, the stem, and the leaves. A portion (150 g) of the roots was weighed and extracted in a blender with deionized water (5 ml/g material) at room temperature. The resulting crude extracts were filtered through Whatman No. 1 filter paper and the remaining liquid was filtered-sterilized using a Millipore 0.22 μm filter.

Determination of dissolved oxygen concentration—We used a Labworks II interface (SCI Technologies, Bozeman, MT) that was connected to a computer with Labworks II software and had two attachments, a dissolved oxygen probe (Zeigler Bros. Inc., Gardners, PA; ANON, ndg) and a thermistor (SCI Technologies, Bozeman, MT). A program was designed in Labworks software to measure the temperature and dissolved oxygen concentration at one-minute intervals (Arnot et al., 1998). The thermistor was calibrated with water at two different temperatures (10 and 25°C). The probe was calibrated at two different temperatures using known values for solubility of dissolved oxygen. Both sensors were placed in a modified 1-L Erlenmeyer flask filled with 600 mL of distilled water and the specimen being tested. The flask was air-tight and had a side septum-stoppered neck that was used for addition of the extracts. The system was placed under fluorescent illumination (120 $\mu E \cdot m^{-2} \cdot sec^{-1}$, as measured by a LI-COR model LI-

TABLE 1. Dissolved oxygen concentration before and after addition of cattail root extract to the microenvironment.

Aquatic Plant	Average dissolved oxygen concentration before addition of extract (mg/L)	Average dissolved oxygen concentration after addition of extract (mg/L)	Reduction in average dissolved oxygen concentration, %
Cabomba caroliniana	18.6 ± 0.0*	18.5 ± 0.0	1.1
Elodea canadensis	32.3 ± 24.7	18.3 ± 12.9	40 ± 6
Hydrilla verticillata	6.0 ± 2.1	8.9 ± 0.1	no inhibition
Myriophyllum spp.	4.7 ± 0.7	2.8 ± 1.6	45 ± 25
Vallisneria spp.	4.0 ± 0.1	2.2 ± 0.2	45

* Mean values ± standard error.

185A photometer). Dissolved oxygen and temperature measurements were collected for ~6 hours. After this period of time, 200 mL of the cattail root extract were added, and data collection proceeded for another 6 hours. Data were collected every minute for the 12-hour period. Data analysis was conducted on data acquired 3 hours prior to addition of extract and three hours after addition of extract allowing 30 minutes after addition for an equilibration period. The mean dissolved oxygen concentration for the first three hours was determined and was assigned a relative concentration of 100%. Then the mean dissolved oxygen concentrations after the addition of extract were determined. Finally, percent inhibition was calculated. The procedure was repeated twice for each plant species. Treated plants were kept in plastic containers under lights in a 12-hour photoperiod for 7 days. After that time, their final fresh weight was determined by means of a Mettler H35 balance (Mettler Instrument Corp., Highstown, NJ) and recorded.

Determination of organic carbon—Organic carbon analyses of the cattail extracts were done using a Dohrmann (model DC-180) automated carbon analyzer. Aqueous extracts used in the dissolved oxygen bioassay were analyzed for organic carbon content. Calibration was done using potassium hydrogen phthalate in deionized water, serially diluted from 2,000 ppm to give a 10-ppm working standard. The concentration of organic carbon was then calculated.

RESULTS AND DISCUSSION—The impact of cattail extracts on the oxygen production of the selected aquatic weeds is summarized in Table 1. For each run, dissolved oxygen concentrations before and after addition of the extract were averaged. An equilibration time of 30 minutes was considered necessary in order to ensure proper mixing and diffusion of the bioactive material.

If nothing else, the study demonstrated the utility of a computer-interfaced continuous data-gathering system that can provide a useful bioassay system. The system is much more convenient than using a Warburg apparatus; for example, data were collected each minute for six hours before and six hours after adding the extracts, and it is hard to imagine a person or persons willing to undertake this activity. It is possible, however, to obtain too many data, owing to the sensitivity of the system. For example, the observer tends to see "natural noise," owing to the competing processes of respiration and photosynthesis occurring simultaneously that can lead to continuous changes in the dissolved oxygen content. By looking at a longer-

TABLE 2. Average fresh weights of treated plants after 7 days of exposure to the cattail extracts.

Aquatic Plant	Average weight of plants before treatment (g)	Average weight of treated plants after 7 days of exposure to the cattail extracts (g)	Change in fresh weight, %
Cabomba caroliniana	20.1 ± 0.2*	18.7 ± 0.9	−7.0
Elodea canadensis	25.4 ± 0.5	21.1 ± 1.2	−1.7
Hydrilla verticillata	20.6 ± 0.9	22.3 ± 1.6	8.3
Myriophyllum spp.	14.3 ± 0.4	10.7 ± 2.0	−25.2
Vallisneria spp.	12.2 ± 0.3	9.0 ± 1.1	−26.3

* Mean values ± standard deviation.

term change, i.e., over a three-hour period, as we did, the short-term changes are damped, and a more general trend appears.

The data indicate that the oxygen production by *Vallisneria spp., Elodea canadensis, Cabomba caroliniana,* and *Myriophyllum spp.* was inhibited by the extract, while *Hydrilla verticillata* was not inhibited under the conditions of this experiment.

More specifically, for *Vallisneria spp., Elodea canadensis,* and *Myriophyllum spp.*, the percent reduction in the average dissolved oxygen concentrations was very similar, approximately 40%. This is consistent with the observed long-term impact of the cattail extracts on those plants. After one week of exposure to the extract, the plants had deteriorated and showed signs of damage. Data for average weight change of the treated plants after 7 days of exposure to the extracts are presented in Table 2.

In contrast, *Cabomba caroliniana* showed very little inhibition, and *Hydrilla verticillata* was not inhibited. Both are known to be very resistant to conventional weed management techniques, so these results are not surprising. In this study, the average total organic carbon of the cattail extracts was 610 ppm. It is possible that inhibition could be achieved by using more concentrated extracts, but such concentrations would not be realistic.

The difference in sensitivity of plants to selected chemicals is hardly new, the most spectacular example is the resistance of hydrilla. An earlier study revealed that hydrilla was not adversely affected by sulfuric acid at pH 3, though fauna were killed (Trent et al., 1978). And the acid solutions adversely affected chara, naiad, and vallisneria.

There is a strong possibility that *Vallisneria spp., Elodea canadensis,* and *Myriophyllum spp.*, could be biologically managed by chemicals derived from cattail root extracts, but other approaches will be required for hydrilla.

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ISOTOPE ANALYSIS OF GALENA FROM PREHISTORIC ARCHAEOLOGICAL SITES IN SOUTH FLORIDA

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ABSTRACT: *Lead-isotope ratio measurements of galena samples from three prehistoric archaeological sites in south Florida indicate a close similarity to the isotopic ratios of galena deposits in southeast Missouri. The isotopic provenance determinations provide supporting evidence for the acquisition by native peoples in Florida of exotic materials from distant locations via trade networks.*

THE mineral galena is occasionally found in prehistoric archaeological sites in Florida (e.g., Archaeological Consultants, Inc., 1994; Austin, 1993; Bullen, 1952; Bullen et al., 1970; Dickel and Carr, 1991; Jones, 1982; Jones and Tesar, 1996; LaFond, 1972; Milanich et al., 1984; Mitchem, 1989; Moore, 1894a, 1894b, 1895a, 1895b, 1901, 1902, 1918; Steinen, 1982; Willey, 1949). It commonly occurs as small cubes, "lumps," or "masses," but was sometimes fashioned into beads or pendants. The sites where galena has been found range in age from the early Woodland through the Historic periods (ca. 500 B.C. to A.D. 1700).

Galena is a mineral consisting of lead sulfide (PbS) that crystallizes isometrically into well-formed cubes. It possesses a metallic luster, perfect cubic cleavage, is relatively soft (2.5 to 2.75 on the Mohs hardness scale), with a specific gravity of 7.4 to 7.5. Galena is the primary mineral in lead and was used by native peoples as a source of white or gray pigment, as a raw material to manufacture beads, pendants, or other objects, and to sprinkle over the dead in mortuary ceremonies. Its appearance in prehistoric sites, along with other exotic materials such as steatite, mica, copper, and crystal quartz, typically has been interpreted as evidence of participation in interregional trade networks (Austin, 1993; Bullen, 1978; Milanich, 1994; Milanich et al., 1984; Sears, 1962; Steinen, 1982). However, with one exception which will be discussed below, there have been no prior attempts to determine the specific provenance of archaeological galenas in Florida.

Previous research on the provenance of galena from North American archaeological sites has been conducted by Farquhar and Fletcher (1980),

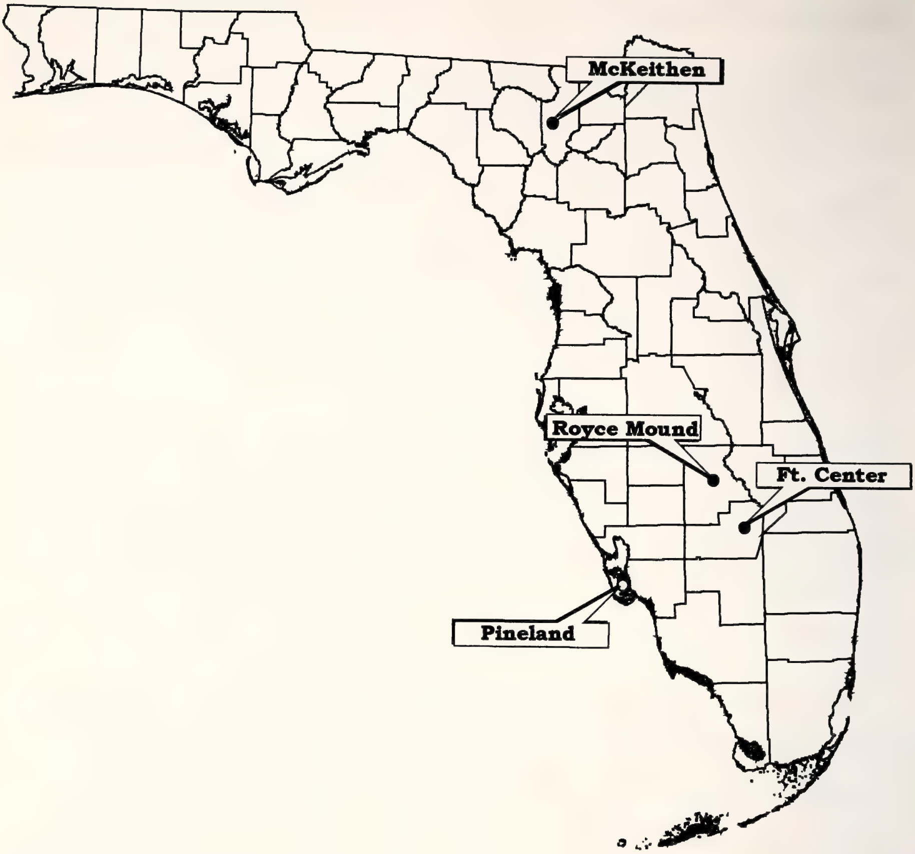

FIG. 1. Locations of archaeological sites in central and south Florida where galenas discussed in the text were recovered.

Farquhar and co-workers (1995), Walthall (1981), and Walthall and co-workers (1979, 1980). Walthall (1981) has discussed the occurrence of galena at prehistoric sites throughout the eastern U.S., and has mapped the major source areas. The closest sources to Florida are in northern Alabama, central Tennessee-central Kentucky, and the east Tennessee-Virginia district, although the most important source areas during prehistory apparently were in Missouri where galena occurs as veins in open-air crevices and caves, or as surface residual deposits (Walthall, 1981).

SAMPLES AND SITE LOCATIONS—Galenas from three prehistoric sites in south Florida (Figure 1) were analyzed to determine their geological provenance. The Royce Mound (8HG676) is located in southern Highlands County, just east of the town of Lake Placid, on the eastern margin of the Lake Wales Ridge overlooking Lake Istokpoga. A cube of galena weighing 43.2 gm was recovered during excavations conducted there in 1992 (Austin, 1993). The mound also contained fragmented human skeletal remains, a small piece of mica, several pendants made of non-local stone (micaceous schist, quartz-rich schist, metamorphic and metavolcanic stone), large bifacially flaked projectile points of non-Florida chert, and two check-stamped pottery vessels. Based on the artifact content, the site is estimated to date to the middle Woodland Period, or ca. A.D. 1–300.

Fort Center (8GL13) is a large earthwork complex located on Fisheating Creek near Lake Okeechobee in Glades County. The site was the focus of a multi-year research project led by William Sears during the late 1960s and early '70s (Sears, 1982). A galena "hemi cone" weighing 4.3 gm was recovered during excavation of Mound A (Steinen, 1982), a habitation mound associated with a nearby platform/burial mound and mortuary pond. Ceramic seriation and radiocarbon dates indicate that Mound A and the rest of the mound-pond complex was in use primarily during the middle Woodland Period (Sears's Period II at Fort Center), or from approximately A.D. 200–600 (Sears, 1982). A number of artifacts recovered from Mound A were made of non-local materials, including granite, diorite, granodiorite, gneiss, and quartz crystal.

The Pineland Site Complex is located near the north end of Pine Island in Lee County. The site consists of several large mounds and middens that date from the early Woodland through Historic periods (referred to in the local chronology as Caloosahatchee I-V), or ca. 500 B.C. through A.D. 1700. Excavations were carried out at this site from 1989 through 1992 (Walker and Marquardt, in preparation). Two pieces of galena were recovered from Brown's Mound (8LL33) within the Pineland Site Complex. The specimen analyzed is a small cube weighing 6.5 gm. It was recovered from post-hole fill in a midden "floor" that has an associated radiocarbon date of A.D. 1280, placing it within the late prehistoric, Caloosahatchee III Period.

The galenas from Fort Center and Pineland are curated at the Florida Museum of Natural History (FLMNH Catalogue Numbers A-15398 [Fort Center] and 92-12-1/5 [Pineland]). The galena from the Royce Mound is in the possession of the landowner, Mr. Raymond Royce of Lake Placid, Florida.

ANALYSIS METHODS—The lead-isotope analysis was conducted at the University of Toronto's Department of Physics. Lead-isotope measurements were made using a conventional solid source mass spectrometer having a 30 cm radius of curvature, 90° deflection, magnetic analyzer. Milligram samples of galena were partially dissolved in hot 10 N ultrapure HCl. The resulting lead chloride was dissolved in water. Approximately one microgram of lead in solution was transferred to a silica gel-phosphoric acid substrate on a single rhenium filament. Lead ions were generated by thermal evaporation in the spectrometer ion source. Mass fractionation corrections to the measured isotopic ratios were based on replicate analysis of lead isotopic standard SRM 981.

Provenance determinations were made by comparing the lead-isotope ratios from the archaeological galenas to similar data for galenas from naturally occurring mineral deposits. Lead contains four isotopes: ^{204}Pb, ^{206}Pb, ^{207}Pb, and ^{208}Pb, and the concentrations of the four isotopes vary by source. The aim of isotope analysis is to establish that an archaeological galena is consistent with derivation from a geologically defined source. This requires that the percent concentrations of all four isotopes in the archaeological example must lie within the data ranges of the source galenas. An equivalent method of comparison uses three isotope ratios. A three-dimensional plot is difficult to visualize in print, so the comparison often is made using two sets of ratio pairs. As one pair we have chosen ^{208}Pb/^{206}Pb and ^{207}Pb/^{206}Pb, a set commonly used in archaeological studies (e.g., Farquhar and Fletcher, 1980). Figure 2 shows these ratios for galenas from three potential mineral sources located in the midwestern United States: the upper Mississippi Valley (UMV), the Illinois-Kentucky area (IK), and the rich and still productive southeast and central Missouri region (SEM-CM). The analyses used to define the isotopic fields for these deposits have been selected from the publications listed in the caption of Figure 2. We have used only those data that can be accurately interrelated by standardization and have corrected some of the published values where this was appropriate. The data sets for the three regions are surrounded by boundary lines that define the limits of the source data fields as determined by the presently available ratios. There are small areas of overlap but in general

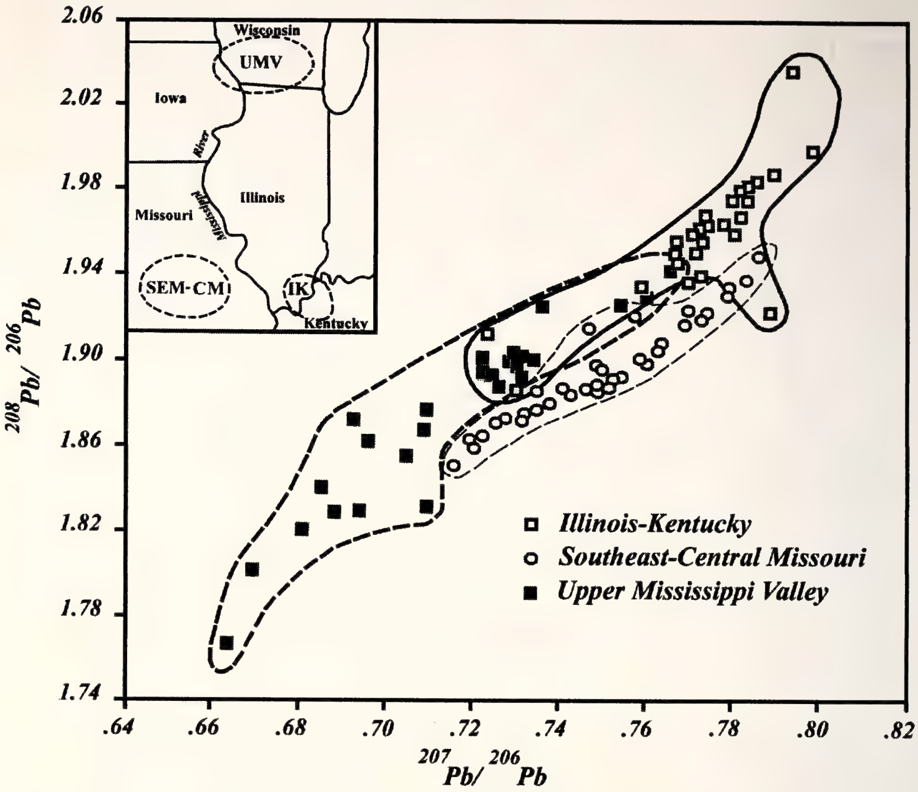

FIG. 2. Bivariate plot of lead-isotope ratios ($^{208}Pb/^{206}Pb$ and $^{207}Pb/^{206}Pb$) for galenas from the upper Mississippi Valley (UMV), Illinois-Kentucky (IK), and southeastern Missouri-central Missouri (SEM-CM). Locations of these regions are outlined on the inset map. Data sources are: Doe and Rohrbaugh (1977), Hart and co-workers (1981, 1983), and Sverjensky and co-workers (1979).

the $^{208}Pb/^{206}Pb$ and $^{207}Pb/^{206}Pb$ ratios serve to identify the sources of the galenas in the majority of cases.

The second isotopic ratio pair chosen as a basis of comparison is $^{208}Pb/^{204}Pb$ and $^{206}Pb/^{204}Pb$. Figure 3 shows these values for the three mineral districts using the same sources listed in the caption of Figure 2. Again, while there are small overlaps in the data fields of the three regions, the source areas are generally well defined by the $^{208}Pb/^{204}Pb$ and $^{206}Pb/^{204}Pb$ ratios.

RESULTS—The measured isotopic ratios for the three archaeological galenas are presented in Table 1. In Figures 4 and 5, the isotopic ratios for the Royce Mound, Fort Center, and Pineland galenas are plotted against the outlines of the data fields for the SEM-CM, UMV, and IK mineral districts. In both figures the data points for all three archaeological galenas fall well within the data field for the SEM-CM deposits and outside those of the UMV and IK mineral regions. Based on comparison with the presently available geological data, the archaeological galenas cannot have been derived from among the UMV or IK deposits while their isotopic ratios are consis-

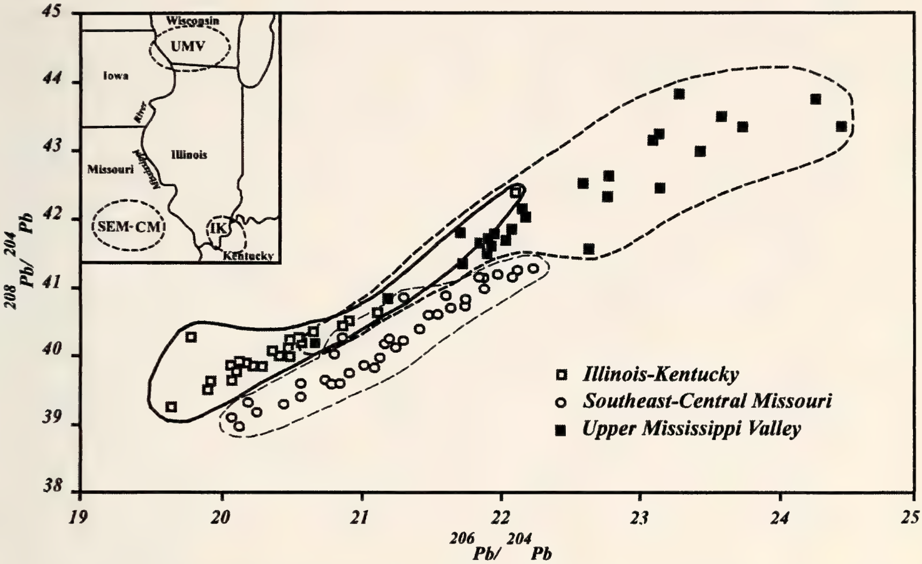

FIG. 3. Bivariate plot of lead-isotope ratios ($^{208}Pb/^{204}Pb$ and $^{206}Pb/^{204}Pb$) for galenas from the upper Mississippi Valley (UMV), Illinois-Kentucky (IK), and southeastern Missouri-central Missouri (SEM-CM). Data sources are the same as those in Figure 2.

tent with an origin in the SEM-CM region. The differences in isotopic composition among the three galena samples are not significant, particularly since there may be large differences in the isotopic composition of galenas from any given ore zone (Hart et al., 1983). However, because the isotopic composition of the Royce Mound and Fort Center galenas are virtually identical, there is a strong possibility that they came from the same mineral deposit.

DISCUSSION—A recent review of the literature has revealed a total of 54 archaeological sites in Florida that have yielded galena or lead artifacts (R. Austin, unpublished data). In addition to the three galenas reported here, a galena cube from the McKeithen site (8CO17) in Columbia County (Mil-

TABLE 1. Lead-isotope ratios of galenas from three archaeological sites in south Florida.

Site number	Site name	Lead-isotope Ratios[a]			
		$^{206}Pb/^{204}Pb$	$^{207}Pb/^{206}Pb$	$^{208}Pb/^{204}Pb$	$^{208}Pb/^{206}Pb$
8HG676	Royce Mound	21.802 ± 0.058	0.7320 ± 0.0009	40.93 ± .17	1.878 ± 0.004
8GL13	Fort Center's Mound A	21.867 ± 0.058	0.7306 ± 0.0012	41.04 ± .10	1.876 ± 0.001
8LL33	Brown's Mound, Pineland	22.005 ± 0.030	0.7261 ± 0.0006	41.01 ± .07	1.863 ± 0.002

[a] 2 σ standard deviations.

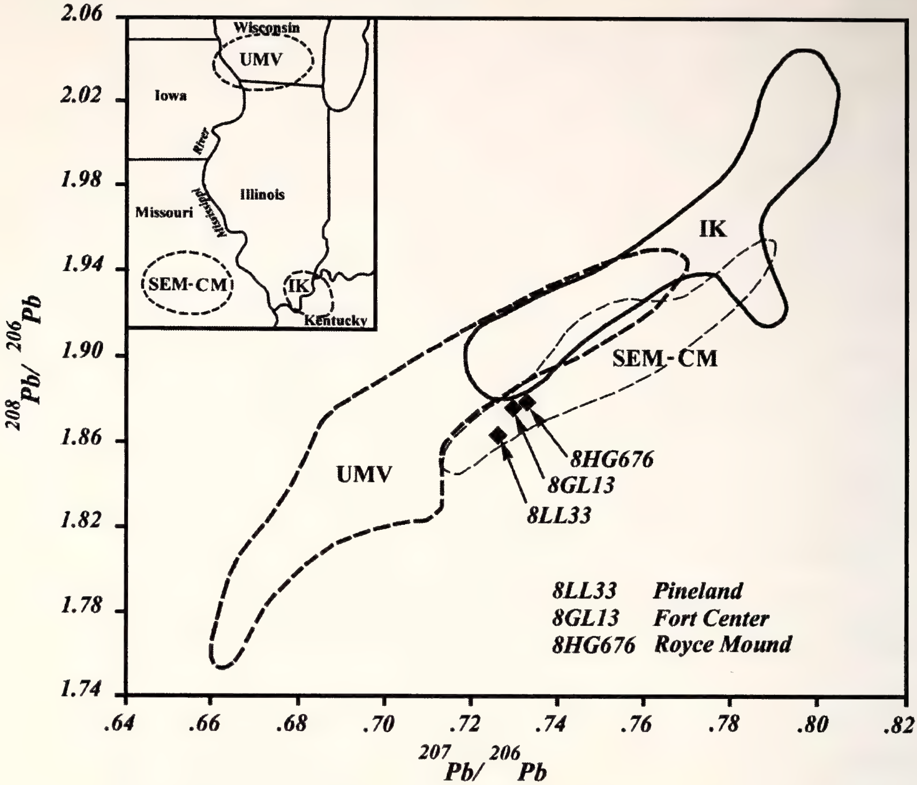

FIG. 4. Bivariate plot of lead-isotope ratios (^{208}Pb/^{206}Pb and ^{207}Pb/^{206}Pb) for archaeological galenas from the Royce Mound, Fort Center, and Pineland. The data field boundaries for galenas from UMV, IK, and SEM-CM are shown for comparison.

anich et al., 1984) previously was sourced to the Potosi mineral district of southeastern Missouri. Its geologic provenance was determined using atomic absorption spectrophotometry to identify trace elements (Walthall, 1981: Appendix II). Thus, the results of analyses of four galena samples all indicate a similar geologic origin. The period of time spanned by the four sites (ca. A.D. 1–1300), their wide geographic distribution (south-central, southwest coast, and north-central Florida), and the varied cultural contexts in which the galenas were found (Belle Glade, Caloosahatchee, and Weeden Island), indicate that trade networks linking Florida native peoples to the Mississippi Valley may have been active for at least a millennium.

Walthall's (1981) analysis of the distribution of galena at prehistoric sites in the southeastern U. S. indicates a major trade route linked the Mississippi Valley region of Illinois and Missouri to communities inhabiting the Flint and Apalachicola rivers of southern Georgia and northwest Florida. From here, galena and other exotic materials may have moved their way to central and south Florida via exchange between communities within geographically

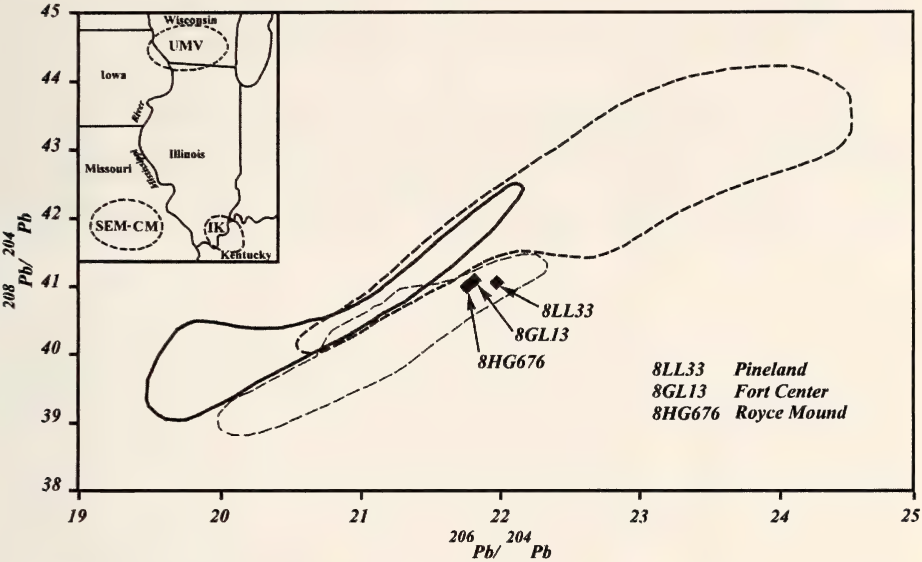

FIG. 5. Bivariate plot of lead-isotope ratios (^{208}Pb/^{204}Pb and ^{206}Pb/^{204}Pb) for archaeological galenas from the Royce Mound, Fort Center, and Pineland. The data field boundaries for galenas from UMV, IK, and SEM-CM are shown for comparison.

circumscribed spheres of interaction. Exchange also would have occurred at the peripheries of these interaction spheres, between neighboring but culturally unrelated groups. There is no archaeological indication that native peoples inhabiting south Florida had direct contact with cultural groups in the Mississippi Valley. Instead, exotic materials from distant locales could have moved into south Florida gradually in a "down-the-line" fashion. Such movement between communities is indicated by the comparatively small amounts of exotic materials, such as galena, that are found at Florida sites. The rarity of these materials contributed to their value, which in turn would have enhanced the status of those who possessed them. The occurrence of galena in burial mounds is further indication of its specialized use in ritual or as a status indicator.

CONCLUSION—Lead-isotope analysis of galenas from three prehistoric sites in south Florida indicates a common source of origin in southeastern Missouri. A fourth galena sample was previously sourced to this region using trace-element analysis. To date these four samples are the only galenas from Florida that have had their geological provenance determined. These results indicate that native peoples in central and south Florida participated in exchange networks that extended northward into the panhandle and eventually to the Mississippi Valley. The movement of galena and other exotic raw materials was especially common during the Woodland Period (ca. 500

B.C.–A.D. 800), but may have continued into the late Prehistoric Period as well.

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Volume 63 Summer, 2000 Number 3

CONTENTS

Remediation of Selenium Contamination by Plants and Microbes: An Annotated Bibliography ....
Kathleen M. Carvalho, Maria T. Gallardo, Melissa J. McGettigan, and Dean F. Martin 133
Temporal Dynamics of Zooplankton Community Composition and Mean Size at Lake Wauberg, Florida ....
Kimberly I. Tugend and Micheal S. Allen 142
An Experimental Analysis of Maze Learning in the Wolf Spider, *Trochosa parthenus* (Araneae: Lycosidae) ....
Fred Punzo 155
Mycorrhizal and Nitrogen-Fixer Associations with *Casuarina* spp. and Mycorrhizal Associations with *Melaleuca quinquenervia* in Everglades National Park ....
Andre J. Cantelmo, Sylvan R. Kaufman, and Jeanmarie Hartman 160
An Approach on Improving the Health of Human Populations ....
Jay W. Palmer 167
Sexual Dimorphism in Vestigial Pelvic Bones of Florida Manatees (*Trichechus manatus latirostris*) ....
Derek M. Fagone, Sentiel A. Rommel, and Meghan E. Bolen 177
Late Pleistocene (Rancholabrean) Records of the Harvest Mouse (*Reithrodontomys*) in Florida ....
Dennis R. Ruez, Jr. 182
Outstanding Student Paper Awards ....
Ernest Estevez 191

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REMEDIATION OF SELENIUM CONTAMINATION BY PLANTS AND MICROBES: AN ANNOTATED BIBLIOGRAPHY

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ABSTRACT: *An annotated bibliography of recent developments in selenium remediation is given. Although many different approaches are considered, the most important processes concerning selenium removal from contaminated soils and waters appear to be microbial-induced chemical reactions that transform the existing selenium species into volatile compounds and accumulation by certain plants.*

SELENIUM is a naturally occurring trace element that is vital to life (Shamberger, 1983) and occurs naturally in essentially all soils and biological materials with quantities varying from 0.005 parts per million (ppm) in a soil-deficient area of Finland to 8000 ppm in the Tuva area of Russia (Berrow and Ure, 1989; Gilon and Potin-Gautier, 1996). Selenium in the human diet is acquired from nutritional sources, the amount of selenium available in foods being dependent on the species and the selenium soil content (MacLeod et al., 1996). However, certain areas of many countries (Australia, Canada, China, Russia, UK, US) have selenium-deficient soils, while other areas have toxic-levels of selenium in the soil (Berrow and Ure, 1989). High concentrations of selenium occur naturally in some soils, especially those derived from Cretaceous shale parent materials (Terry and Zayed, 1998). Both extremes are troublesome. Selenium deficient soils can lead to selenium deficient diets (Keshan disease); too much selenium can lead to selenium toxication (devil's disease in humans, blind staggers in affected cattle).

Excess selenium build up in soil or water can be troublesome, e.g., Kesterson Reservoir of California, and lead to the need for remediation. One of the most environmentally friendly ways to remove this excess selenium would entail using naturally occurring plants and microorganisms to remove the selenium. The use of plants and microorganisms that can naturally volatilize the selenium and remove it from the soil or water has been studied with promising results.

Aquatic plants have been used in water treatment as a means for water quality improvement by transfer and accumulation of metals and excessive nutrients into the biomass. This process is known as phytoremediation. Phytoremediation is an innovative technology that utilizes the natural properties of plants in engineered systems to remediate contaminated sites. Evapotranspiration by plants provides a solar-driven pump-and-treat system, which brings contaminants to the rhizosphere and helps contain them for removal from the site (Erickson et al., 1994).

Some aquatic plants, such as water hyacinths, have been in use for years for secondary sewage treatment (Scarsbrook and Davis, 1971; Ornes and Sutton, 1975), and to remove excess nutrients from eutrophic waters (Dunigan et al., 1975). Water hyacinths can also remove and retain heavy metals from aquatic systems (Cooley and Martin, 1977).

A phytoremediation system capitalizes on the synergistic relationships among plants, microorganisms, water, and soil that have evolved naturally in wetlands and upland sites over millions of years. In the biological sequences that transform contaminants to harmless compounds, plants contribute inherent enzymatic and uptake processes that can recycle or sequester the contaminants they encounter. Plants act as hosts to aerobic and anaerobic microorganisms, supplying them with physical habitat and chemical building blocks. Plant roots and shoots increase microbial activity in their direct environment by providing additional colonizable surface area, increasing readily degradable carbon substrates, and creating temporally and spatially variable oxygen regimes (Jewell, 1994).

Five mechanisms by which plants are believed to remove, degrade, or stabilize environmental contaminants have been proposed. Plants may take up and assimilate contaminants (phytoaccumulation), volatilize the contaminants into the atmosphere (phytovolatilization), or degrade the contaminants within plant tissues using enzymes (phytodegradation). In the rhizosphere of some plants, released plant exudates and enzymes that stimulate biochemical activities may enhance the biodegradation of environmental contaminants (rhizodegradation). For metals, plants may be used to absorb and precipitate large quantities of toxic metals in soils, thus reducing their bioavailability and preventing their entry into ground water and food chains (phytostabilization) (Flathman and Lanza, 1998). In the absence of soil, different phytoprocesses may take place. Under these intensive conditions, free from interference by soil chemicals and soil-borne microorganisms, plants can function as bioreactors and accomplish very efficient transformations (Nzengung et al., 1999).

In this paper, we review the research efforts that have been made to establish bio- and phytoremediation as a new technology for the cleanup of selenium pollution in soil and water. We have included research dealing with selenium removal from soils by plant uptake and accumulation, selenium removal by plant volatilization, selenium removal in the rhizosphere, selenium removal by wetlands, and selenium-volatilizing plants. Clearly, it would be difficult to have covered every paper related to remediation of selenium written in the past ten years, therefore, we have made an effort to include as many representative papers as we could.

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AZAIZEH, H. A., S. GOWTHAMAN, AND N. TERRY. 1997. Microbial selenium volatilization in rhizosphere and bulk soils from a constructed wetland. J. Environ. Qual. 26(3): 666–672.

San Francisco Bay is a well-known site for selenium contamination. The wastewater discharged into the bay from oil refineries is mainly responsible for the source of toxic selenium. Chevron USA, Inc. constructed a 36-ha wetland at Richmond, CA, in an attempt to reduce the harmful concentrations of selenium. This study focuses on the role of microbes in selenium volatilization from wetlands as a means of cleanup. The first objective was to determine whether fungi or bacteria were the dominant wetland organisms to volatilize selenium. Microbial samples were isolated from the rhizosphere and tested against samples supplemented with fungicide and samples supplemented with bactericides. Atomic absorption methods showed that bactericides were more effective than the fungicide in significantly reducing the rate of Se volatilization. The high correlation ($r = 0.89$) between total bacteria present in the culture solutions and the amount of Se volatilized indicated that bacteria were the main contributors to selenium volatilization in wetland environments.

BANUELOS, G. S., H. A. AJWA, B. MACKEY, L. WU, C. COOK, S. AKOHOUE, AND S. ZAMBRUZUSKI. 1997. Evaluation of different plant-species used in phytoremediation of high soil selenium. J. Environ. Qual. 26(3): 639–646.

The search for effective Se-accumulator plant species is an integral part of phytoremediation. Based on previous studies, the following species were selected for evaluation of selenium uptake: *Brassica napus* (canola), *Hibiscus cannabinus* (kenaf), and *Festuca arundinacea* (tall fescue). The growth effect of high concentrations of Se was also examined by dry matter yield measurements. Results showed that canola accumulated the highest concentrations of Se among the three species, having leaf concentrations as high as 470 mg Se/kg dry matter. Kenaf and tall fescue had lower leaf concentrations with the range of Se between 45 to 50 mg/kg dry matter. A very important finding of this study, however, was that growth height of canola and kenaf were visually stunted. Canola yield was reduced by an average of 25%, and kenaf was reduced by 27%. It is possible that phytoremediation will be the primary means of removing chemical pollutants, but will not come without some negative side effects. The authors concluded that canola removed 57% of the total selenium lost, and was the most efficient of those plants studied for lowering soil Se concentrations.

Banuelos, G. S., H. A. Ajwa, N. Terry, and A. Zayed. 1997. Phytoremediation of selenium laden soils: a new technology. J. Environ. Qual. 52(6): 426–430.

The authors presented an in-depth analysis of the mechanism of phytoremediation and its function in reducing high concentrations of selenium in soil. The results from a phytoremediation study in 1989 led Banuelos and his colleagues to hypothesize that the plant genus *Brassica* has a better capacity to absorb selenium because of the chemical similarity it has to sulfur. *Brassica spp.* are known sulfur-accumulating plants, and the process by which they absorb sulfate ions can also be used to absorb selenate ions. A follow-up study showed a net reduction of almost 40% in total soil selenium inventory to a depth of 60 cm. Mass-balance calculations provided evidence that Se was lost through different forms (such as volatilization), since not all of the Se was accounted for in the plant tissues. Presumably, selenium-accumulator plants resist selenium toxicity because they do not incorporate the Se into proteins. These plants have the selective ability to avoid synthesizing selenomethionine. If this selenoamino acid is used to code for a protein, or modify the seleno-compound to a derivative that cannot be incorporated into a protein, the plant will fail to develop and function properly.

Research of phytoremediation for Se-contaminated soil has shown that phytovolatilization is an important component of the removal of selenium. Selenium volatilization rates have proven to be species-dependent. The most effective Se-volatilizers among agricultural crops were rice, broccoli, and cabbage. These species were able to volatilize Se at rates of 1.5 to 2.5 mg/kg dry matter/day. This is an important finding, leading to another area of phytoremediation. There is perhaps great benefit to be gained from agricultural crops as phytoremediators, and Se supplementation for human consumption.

Banuelos, G. S., H. A. Ajwa, Wu, X. Guo, S. Akohoue, and S. Zambruzuski. 1997. Selenium-induced growth reduction in brassica land races considered for phytoremediation. Ecotox. Environ. Saf. 36(3): 282–287.

Brassica juncea (Indian mustard) has been found to accumulate high concentrations of selenium. If this species is to be considered for phytoremediation purposes, it is necessary to examine the physiological and biochemical effects that toxic levels of selenium induce. Growth characteristics (dry matter yield and leaf surface area) were found to be significantly reduced for all of the land races grown in selenium-enriched water culture. Protein content was nearly 5% lower in the shoots of the experimental species. It was suggested that plants with high tolerance to toxic concentrations of selenium are unable to discriminate between selenate and sulfate. Thus, selenate may be utilized in the plant's sulfur pathway. The assimilation of selenate results in selenium incorporation into methionine and cysteine. Proteins with such alterations are likely to differ in stability and catalytic and regulatory properties. Further research is needed to determine the long-range effects on the habitats in which phytoremediation is employed.

Banuelos, G. S., H. A. Ajwa, L. Wu, and S. Zambruzuski. 1998. Selenium accumulation by *Brassica napus* grown in Se-laden soil from different depths of Kesterson Reservoir. J. Soil Contam. 7(4): 481–496.

Brassica napus (canola) was used to accumulate selenium from soils from the Kesterson Reservoir. While accumulation of selenium under controlled greenhouse conditions has been studied, it is important to be able to see how selenium accumulator plants will perform under field conditions. In this study, *Brassica napus* was evaluated as a selenium accumulator in both greenhouse and field conditions. Sediment from three different depths, 0–30, 30–60, and 60–90 cm, from Pond 2 in the Kesterson Reservoir were taken with initial selenium concentrations ranging from 10 to 112 mg/ kg. Plants were allowed to grow in the selenium-contaminated soil for one year. At the end of the year, soil and plant samples were analyzed for selenium content.

In the greenhouse study, selenium loss in the soil was as high as 24%, and the shoot concentrations were 180, 53, 19 mg/ kg dry weight at 0–30, 30–60, and 60–90- cm samples, respectively. In the field study, the highest amount of selenium in the soil was 26 mg Se/ kg, and the canola grown in the field accumulated approximately 50 mg Se/ kg dry weight. When comparing the greenhouse and field experiments using *Brassica napus* for phytoremediation, the authors concluded that when using the selenium-contaminated soils, a greenhouse study gave a 50% greater accumulation of selenium than did the field study.

De Souza, M. P., E. A. H. Pilon-Smits, C. M. Lytle, S. Hwang, J. Tai, T. S. U. Honma, L. Yeh, and N. Terry. 1998. Rate-limiting steps in selenium assimilation and volatilization by Indian mustard. Plant Physiol. 117(4): 1487–1494.

Brassica juncea (Indian mustard) has been shown to be a good candidate for Se phytoremediation because it can accumulate high concentrations of Se in its tissues, and it produces a large biomass. Indian mustard has also been identified as an effective Se-volatilizing plant species. Volatilization is attractive as a method for removal of selenium-contaminated sites because toxic organic and inorganic forms of Se are converted to less harmful gaseous forms. Selenium volatilization ensures that toxic forms are permanently removed from the contaminated site and its associated food chain. This study used Indian mustard to examine the factors that control uptake, translocation, and volatilization of selenium from selenate and selenite. Results showed that Se accumulation in tissues and the rate of Se volatilization increased linearly with the length of time of pretreatment for both selenate and selenite. Plants supplied with selenite showed a rate of Se volatilization at least twice as great than plants supplied with selenate. The rate of uptake, however, was significantly higher for selenate than for selenite. Selenate was rapidly translocated to the shoot, whereas only about 10% of the selenite was translocated. Analysis of x-ray absorption spectroscopy revealed that selenite-supplied plants accumulated organic Se, most likely in the form of selenomethionine, whereas selenate-supplied plants accumulated selenate. The authors concluded that the rate of selenate reduction, as well as the availability of Se in roots, was related to uptake and translocation limits of Se volatilization from selenate. This study gave evidence that Se volatilization from selenite is limited by selenite uptake and by the conversion of selenomethionine to dimethylselenide.

Ehrlich, H. L. 1997. Microbes and metals. Appl. Microbial. Biotechnol. 48(6): 687–692.

In conjunction with the industrial exploitation of plants for phytoremediation, microbes are being studied as a possible treatment for dangerously high concentrations of metals and metalloids. Prokaryotic organisms have been found to oxidize selenite and selenium in its elemental form. *Theauera selenatis,* a eubacterium, reduces selenate and selenite to elemental selenium for the utilization as electron donors or acceptors in energy metabolism. Studies have also shown that certain forms of fungi can convert oxidized selenium to volatile methylated selenides, which can then escape into the atmosphere. Although there exists a natural interaction between microbes and metal species, these organisms are capable of accumulating excess amounts, often without detriment. Like some plant species used in selenium uptake, the ability of various microbes to detoxify selenium by methylation is being strongly considered for reducing toxic levels in the ecosystem.

Flurry, M., W. T. Frankenberger, Jr., and W. A. Jury. 1997. Long-term depletion of selenium from Kesterson dewatered sediments. Sci. Total Environ. 198: 259–277.

In 1987, Flurry and co-workers studied part of the Kesterson Reservoir; specifically they established a field of 21 × 27 meters in the dewatered Pond 4. A study to monitor the depletion of selenium from the soil was conducted over a period of 100 months, and it was observed that 68–88% of the total amount of selenium had been dissipated from the topsoil. The authors believed that a majority of the selenium was converted into volatile dimethylselenide $(CH_3)_2Se$ by microbial methylation. Periodically tilling and irrigating the soil, as well as addition of protein amendments, enhanced the microbial activity. It had already been observed that the production of gaseous forms of selenium are influenced by temperature, soil air and moisture content, specific carbon and protein amendments, and soil management (Thompson-Eagle and Frankenberger, 1992). There was no correlation between the depletion of selenium in the soil and rainfall or temperature. It was suggested, however, that depletion of selenium in the winter months was due to leaching, because of high rainfall amounts, and depletion of selenium in the summer was primarily due to volatilization. The highest amount of selenium depletion was observed when the soil was amended with the protein casein, although this was not found to be statistically significant.

The authors also suggested two models to describe the long-term kinetics of selenium depletion in the soil. The first model was a two-compartment model, consisting of one compartment containing the insoluble selenium in the soil, and the other compartment consisting of the soluble selenium in the soil. The latter compartment was assumed to have the only species that underwent microbial volatilization and leaching. The second model was a one-compartment model, for which the rate-limiting step for conversion of insoluble selenium species to soluble forms is ignored. It was concluded that the two-compartment model was superior to a one-compartment model when applied to the data acquired from the experiment.

HANSEN, D., P. J. DUDA, A. ZAYED, AND N. TERRY. 1998. Selenium removal by constructed wetlands: role of biological volatilization. Environ. Sci. Technol. 32(5): 591–597.

San Francisco Bay, the site of discharge from six oil refineries, was polluted with high concentrations of selenium. A constructed wetland adjacent to the Bay was found to significantly reduce the levels of selenium from 20–30 micrograms per liter present in the incoming water, to less than 5 micrograms per liter in the exiting water. A major focus of this study was selenium volatilization as a means of phytoremediation. Volatile forms of selenium are relatively nontoxic, and correlate to minimizing plant-bound selenium available to wildlife. Results showed that brass buttons (*Cotula coronopifolia*) and saltgrass (*Distichlis spicata*) sites were most effective for volatilization. The study also gave evidence that shoot removal leads to substantially increased rates of selenium volatilization by the remaining root system.

LOSI, M. E. AND W. T. FRANKENBERGER, JR. 1997. Bioremediation of selenium in soil and water. Soil Sci. 162(10): 692–702.

The authors provided an explanatory review of selenium and the threat it poses to wildlife when found in high levels, as well as the possible techniques for bioremediation. Most soils contain from 0.01 to 2 mg Se/kg, but various factors, both naturally occurring and man-induced, can lead to high concentrations. Petroleum refining and anthropogenic activities such as irrigated agriculture and mining can disturb the natural distribution of selenium. Soil parent material, climate, topography, and age of soil also affect the Se concentration of soil. Fresh waters generally contain concentrations of 0.1 to 100 μg Se/L, but rarely exceed 10 μg/L. Drainage waters near San Joaquin Valley, CA have been found to contain toxic levels of Se, with concentrations generally ranging between 400 and 1000 μg/kg and measuring as high as 4200 μg Se/L. The California Water Resources Control Board has designated the safe Se concentration limit to be 2–5 μg/L in rivers and wetlands receiving agricultural drainage water. Microbial reduction of Se has been studied as a possible mechanism for lowering high concentrations. Selenate can be reduced by microbes in respiratory metabolism yielding insoluble elemental Se, the terminal electron acceptor. This reaction has been observed with selenite; however the reaction does not support growth. Microorganisms also have the ability to volatilize methylated Se, a naturally occurring defense against toxicity. Bacteria and fungi transform toxic species of Se, such as selenate and selenite, into less harmful volatile dimethylselenide. Isolating such species and developing efficient and cost-effective technology for bioremediation is needed.

Pilon-Smits, E. A. H., M. P. De Souza, G. Hong, A. Amini, R. C. Bravo, S. T. Payabyab, and N. Terry. 1999. Selenium volatilization and accumulation by twenty aquatic plant species. J. Environ. Qual. 28: 1011–1018.

The use of 20 different aquatic plants as agents for phytoremediation of selenium from industrial or agricultural wastewater was addressed in this paper. It is known that aquatic plants are able to remove selenium by accumulation and volatilization. The following 20 different plants were supplied 20 μM solutions of selenate or selenite under controlled conditions and then compared: azolla (*Azolla caroliniana* Willd.), baltic rush (*Juncus balticus* L.), cattail (*Typha latifolia* L.), fuzzy water clover (*Marsilea drummondii* Add. Brown), hardstem bulrush (*Scirpus acutus* Muhl.), iris-leaved rush (*Juncus xiphioides*), Louisiana iris (*Iris louisiana* hybr.), mare's tail (*Hippuris vulgaris* L.), Mexican sprangletop (*Leptochloa uninervia* Hichc. and Chase), monkeyflower (*Mimulus guttatus* Fisch. ex. DC.), parrot's feather (*Myriophyllum brasiliense* Camb.), saltgrass (*Distichlis spicata* L. Greene), saltmarsh bulrush (*Scirpus robustus*), smartweed (*Polygonum hydropiperoides* Michx.), spikerush (*Eleocharis obtusa* Willd. Schult.), umbrella plant (*Cyperus alternifolius* L.), water forget-me-not (*Myosotis scorpioides* L.), water hyacinth (*Eichhornia crassipes* Mart. Solms.), water primrose (*Ludwigia repens* Forst.), and water zinnia (*Wedelia trilobata*). Several important conclusions were obtained from this study. First, regardless of the type of selenium supplied, there was a 50-fold variation among the plants studied. Second, the plants that were the best at volatilization of selenite were also the best for volatilization of selenate. Third, the rate of volatilization of selenite was twice that for selenate with more selenate being translocated into the plant tissues than selenite. Finally, several plants showed accumulation and volatilization rates comparable with *Brassica juncea,* the best known plant for phytoremediation of selenium, including: parrot's feather (*Myriophyllum brasiliense* Camb.), iris-leaved rush (*Juncus xiphioides*), cattail (*Typha latifolia* L.), and saltmarsh bulrush (*Scirpus robustus*).

Raskin, I., R. D. Smith, and D. E. Salt. 1997. Phytoremediation of metals using plants to remove pollutants from the environment. Current Opinion Biotechnol. 8(2): 221–226.

Raskin and colleagues defined phytoremediation as the use of green plants to remove pollutants from the environment or to render them harmless. Although the concept of phytoremediation is not new, it has recently become the topic of extensive research throughout several disciplines. The development of technology and the increased knowledge of phytoremediation mechanisms have led to specific subsets of metal phytoremediation. These include phytoextraction, phytofiltration, phytovolatilization, and phytostabilization. Phytovolatilization, in which plants extract volatile metals, is thought to be a rather promising method for the removal of selenium from a polluted environment. Toxic metals such as selenium can be biomethylated to form volatile molecules that can be lost to the environment. Microbes play a large role in the volatilization of selenium, and plant species have been found to posses the same ability. *Brassica juncea* (Indian mustard) has been discovered to be very efficient in the removal of Se from soil. The major mechanism used by plants for removal of Se is the volatilization in the form of methyl selenate. However, some plant species can accumulate nonvolatile methyl selenate derivatives in the foliage. Such selenium accumulator plants are being studied for their effectiveness in treating polluted soils. Recently, the enzyme responsible for the formation of methyl selenocystine was isolated from *Astragalus bisculatus.*

Zayed, A., S. Gowthaman, and N. Terry. 1998. Phytoaccumulation of trace elements by wetland plants: I. Duckweed. J. Environ. Qual. 27: 715–721.

Zayed and co-workers examined the use of duckweed (*Lemna minor*) as a potential wetland plant to remove toxic trace elements. It had been shown by Baker in (1981) and Rosenfeld and Beath (1964), that some plants have the ability to absorb and even hyperaccumulate trace elements in their tissues. Therefore, because of this and recent studies exploring the use of constructed wetlands to remove toxic trace elements, Zayed and co-workers experimented with duckweed as a potential accumulator of several different trace metals. The trace elements explored were cadmium (Cd), chromium (Cr), copper (Cu), nickel (Ni), lead (Pb), and selenium (Se) with concentrations ranging from 0.1 to 10 mg/ L of solutions of cadmium sulfate, potassium chromate, copper sulfate, lead nitrate, nickel sulfate, and sodium selenite. The trace element solutions were each individually added to quarter strength Hoagland's nutrient medium containing approximately two grams of duckweed. After eight days of exposure to each element, duckweed was a good accumulator for Cd, Se, and Cu, accumulating 13.3g Cd/kg, 4.27 g Se/kg, and 3.36 g Cu/kg. A toxic effect was observed for all elements except Cr at concentrations higher than 5 mg /L for Cu, 2 mg /L for Se, Pb, and Cd, 10 mg/ L for Ni. There was also a percent growth reduction observed at concentrations of 10 mg/ L for all elements explored. Based on the experimental data, it can be concluded that duckweed is a good potential accumulator for Cd, Se, and Cu.

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TEMPORAL DYNAMICS OF ZOOPLANKTON COMMUNITY COMPOSITION AND MEAN SIZE AT LAKE WAUBERG, FLORIDA

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ABSTRACT: *Patterns of mean zooplankton abundance were observed during January–August 1998 in Lake Wauberg, Florida. Zooplankton size structure was evaluated from April–August. Total zooplankton density, cladoceran density, copepod density and rotifer density varied significantly among months (*$P < 0.01$*). Zooplankton abundance was lowest in January and February, peaked in April and May, then declined throughout the summer. Cladocerans peaked in abundance in May and were dominated by* Daphnia, Eubosmina, Bosmina, *and* Diaphanosoma *at varying times throughout the study. Mean length for cladocerans ranged from 0.30 mm to 0.52 mm depending on which genera dominated at any given time. Mean copepod abundance varied among months and was generally highest in spring. Mean copepod length did not vary significantly (*$P > 0.05$*) among months due to the dominance of nauplii (>70% by number). Mean rotifer density in May was significantly higher than all other months except April (*$P < 0.05$*) with* Conochilus/Conochiloides *(grouped together) and* Brachionus *comprising the dominant taxa. Rotifers ranged in size from 0.06 mm to 0.15 mm and monthly mean size was greatest in late summer due to the presence of larger-bodied rotifers. Our results suggest that Lake Wauberg is more characteristic of tropical systems containing smaller adult cyclopoid and daphnid species than those found in more temperate climates. Fish predation may also play a role in structuring the zooplankton community in Lake Wauberg.*

ZOOPLANKTON communities are dynamic and may change in accordance with environmental conditions (e.g., Hazelwood and Parker, 1961,1963; Makarewicz and Likens, 1979; Beaver and Havens, 1996). Many factors contribute to the size structure and/or species composition of zooplankton communities, including chlorophyll concentration (Patalas, 1972; Brezonik et al., 1984; Beaver and Havens, 1996; Canfield and Jones, 1996), predation (Wells, 1969; Blancher, 1984; Guest et al., 1990; Miller et al., 1990; DeVries and Stein, 1992; Hambright and Hall, 1992; Masundire, 1994; Hessen et al., 1995; Taylor and Carter, 1997; Torres-Orozco and Zanatta, 1998), temperature (Patalas, 1972; Blancher, 1984), and water chemistry (Patalas, 1972; Brezonik et al., 1984; Masundire, 1994). Multiple factors may operate simultaneously, changing on an instantaneous, seasonal, or annual basis. Several studies with multiple collection years have found variation in zooplankton abundances and community composition across years (e.g., Billets and Osborne, 1985; Pope and Willis, 1998).

Zooplankton population size and species composition also varies with latitude. Bays and Crisman (1983) reported that tropical cladocerans consist of smaller species dominated by daphnids, bosminids, moinids, *Ceriodaphnia* and *Diaphanosoma* as compared to temperate lakes. Blancher (1984) found that the abundance of crustacean zooplankton in the Great Lakes was greater than in Florida lakes of similar trophic state and attributed this to differences in temperature and predation by fish. However, we found no studies that addressed differences in rotifer size or abundance between tropical and temperate lakes.

Understanding zooplankton community dynamics is important because the availability of certain species and sizes of zooplankton may affect growth and recruitment of young fishes (Mills et al., 1989; Miller et al., 1990). DeVries and Stein (1992) found that gizzard shad *Dorosoma cepedianum* reduced crustacean zooplankton abundance causing a food limitation for larval bluegill *Lepomis macrochirus.* Unlike gizzard shad, larval bluegill selected larger zooplankton with increasing fish size (Bremigan and Stein, 1994). Black crappie *Pomoxis nigromaculatus* also select for large zooplankton as they grow in early life (Pope and Willis, 1998).

Our objectives were to evaluate temporal patterns of zooplankton abundance, community composition, and mean size at Lake Wauberg, Florida. Patterns of abundance were compared with studies conducted on other lakes of varying trophic states. Previous studies conducted in more temperate systems were used to compare latitudinal effects on zooplankton size patterns.

MATERIALS AND METHODS—*Study site*—Lake Wauberg is a 100-ha natural lake located south of Gainesville, Florida (29°31.53′ N lat., 82°18.12′ W long.). The lake is alkaline with a pH of 7.9 (Florida LAKEWATCH, 1997) and has an average depth of 3.6–3.8 m (Canfield and Hoyer, 1992; Blancher, 1984, respectively). Historical data from March 31, 1990 to December 22, 1996 indicated mean total phosphorus concentration of 107 μg/L (range 56–157 μg/L), mean total nitrogen concentration of 1726 μg/L (range 1230–2403 μg/L), mean chlorophyll concentration of 83 μg/L (range 30–180 μg/L), and mean secchi depth of 0.6 m (range 0.3–0.9 m) (Florida LAKEWATCH, 1997). Lake Wauberg is plankton dominated with aquatic macrophytes (mainly *Eichhornia crassipes, Pontederia cordata,* and *Nuphar luteum*) inhabiting a percent area coverage (PAC) of <1% (Canfield and Hoyer, 1992).

Zooplankton samples—Three zooplankton samples were taken monthly from January–August 1998 using a 64-μm mesh Wisconsin-style plankton net. The plankton net was deployed at three randomly selected stations each month in offshore areas of the lake and towed vertically from the lake bottom to the surface. The depth of each station was recorded to the nearest 0.25 m. Each zooplankton sample was preserved in 10% buffered formalin acetate.

At the laboratory, total volume of each sample for the three stations was measured to the nearest milliliter. Three 1-ml subsamples were then taken for zooplankton counts and size measurements (nearest 0.01 mm). Counts and measurements were conducted with a compound light microscope equipped with an optical micrometer at 100× magnification. Cladocerans and rotifers were identified to genus, and copepods were identified as either calanoid, cyclopoid, or nauplii according to Pennak (1989). All unidentified organisms were listed as "other" under their perspective subgroups (i.e., cladoceran, copepod, rotifer) provided such could be determined. Zooplankton from January–March samples were counted, but not measured for size.

TABLE 1. List of the zooplankton organisms collected at Lake Wauberg from January–August, 1998. Unidentified cladocerans and rotifers accounted for <2% of all organisms collected.

Classification		
Rotifer	Cladocera	Copepoda
Anuraeopsis	*Alona*	Calanoid
Asplanchna	*Bosmina*	Cyclopoid
Brachionus	*Ceriodaphnia*	Nauplius
Conochiloides	*Chydorus*	
Conochilus	*Daphnia*	
Filinia	*Diaphanosoma*	
Hexarthra	*Eubosmina*	
Kellicottia	Immature	
Keratella		
Polyarthra		
Synchaeta		
Tetramastix		
Trichocerca		

Beginning in April, all zooplankton in each subsample were measured to the nearest 0.01 mm. For rotifers, body length was determined excluding the length of spines when appropriate (e.g., *Brachionus, Filinia, Keratella*). Cladocerans and copepods were measured in the same manner described in Canfield and Jones (1996).

Zooplankton density (D) for each sample was determined as:

$$D = (n_s \cdot v_s)/(0.0113 \cdot d) \tag{1}$$

where n_s was the total number of organisms counted in the subsample, v_s was the total volume of that sample in ml, d was the station depth (m), and 0.0113 was the mouth area (m^2) of the zooplankton net. Densities of the three stations were then averaged to obtain mean density for each sample date.

Data analysis—We used one-way analyses of variance (ANOVA) to test for differences in total zooplankton density, copepod density, cladoceran density, and rotifer density among months. Because density values were nonnormal, we used a $\log_{10}$ transformation for each observation prior to analyses. If significant differences ($P \leq 0.05$) were found in ANOVAs, we used the Ryan-Einot-Gabriel-Welsch multiple range test procedure (option REGWQ, SAS, 1996) to identify significant differences among means. The REGWQ multiple-range test controls the Type-I experiment-wise error rate when indicating differences among means.

Similarly, we used one-way ANOVAs to test for difference in mean length of copepods, cladocerans, and rotifers among months. Distributions of mean lengths did not differ from normality, so no transformations were required. If significant differences ($P \leq 0.05$) were found in ANOVAs, we used the Ryan-Einot-Gabriel-Welsch multiple-range test procedure (option REGWQ, SAS, 1996) to identify significant differences among means.

RESULTS—Table 1 lists the zooplankton that were collected and identified in this study (January–August 1998). During the same period, total phosphorus, total nitrogen, chlorophyll *a*, and secchi depth averaged 226 μg/L (range 142—303 μg/L), 1408 μg/L (range 1190—1893 μg/L), 66 μg/L

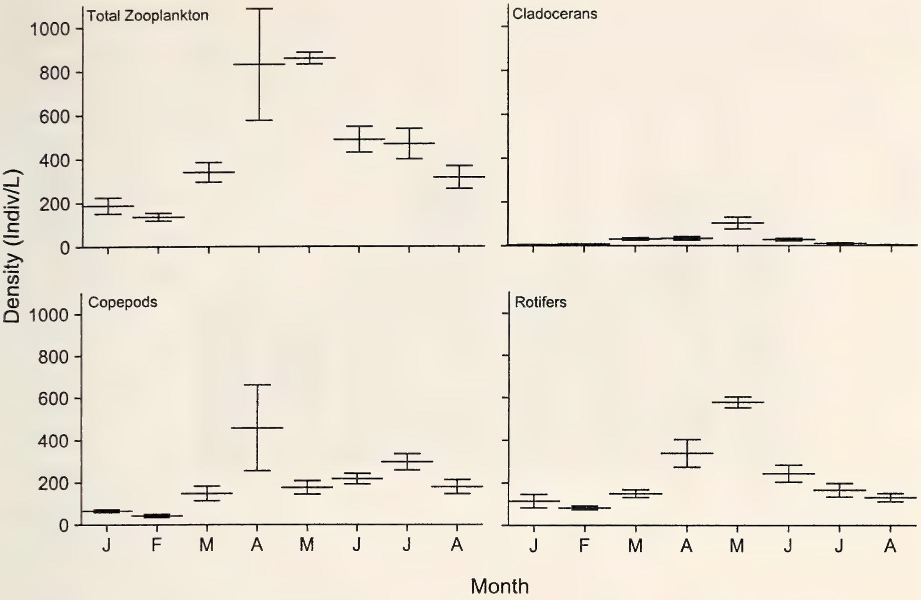

FIG. 1. Mean monthly densities (+ 1 SE) for all zooplankton combined (top left panel), copepods (bottom left panel), cladocerans (top right panel), and rotifers (bottom right panel).

(range 51—120 µg/L), and 0.7 m (range 0.5–0.9 m), respectively (unpublished data, Florida LAKEWATCH).

Patterns of abundance—Total zooplankton density varied significantly among months (ANOVA, $P < 0.01$). Total zooplankton abundance increased in the spring (January–March), peaked in April and May, then declined throughout the summer (June–August) (Fig. 1).

Cladoceran community structure was dynamic and differed among months (ANOVA, $P < 0.01$). Cladoceran density increased through spring and declined during summer, with a peak occurring in May (102 indiv/L; Fig. 1). Cladocerans comprised 1–12% of the zooplankton community over the study period (Fig. 2). *Daphnia* dominated the cladoceran community from January–March (>50% by number, Fig. 3) peaking in abundance in March (29 indiv/L). *Bosmina* and *Eubosmina* were co-dominant (combined, >50% by number) in May (33 and 34 indiv/L, respectively; Fig. 3), but *Eubosmina* was replaced by *Diaphanasoma* in June which comprised 47% of the cladoceran community. *Diaphanasoma* was the only cladoceran present in late summer (July–August) but at relatively low densities (≤9 indiv/L). *Alona* and *Chydorus* were intermittently present and never comprised ≥10% of the cladoceran community. *Ceriodaphnia* was only collected in April and May (<5 indiv/L) and immature cladocerans were collected in May (19 indiv/L) and June (3 indiv/L).

Copepod densities also varied among months (ANOVA, $P < 0.01$).

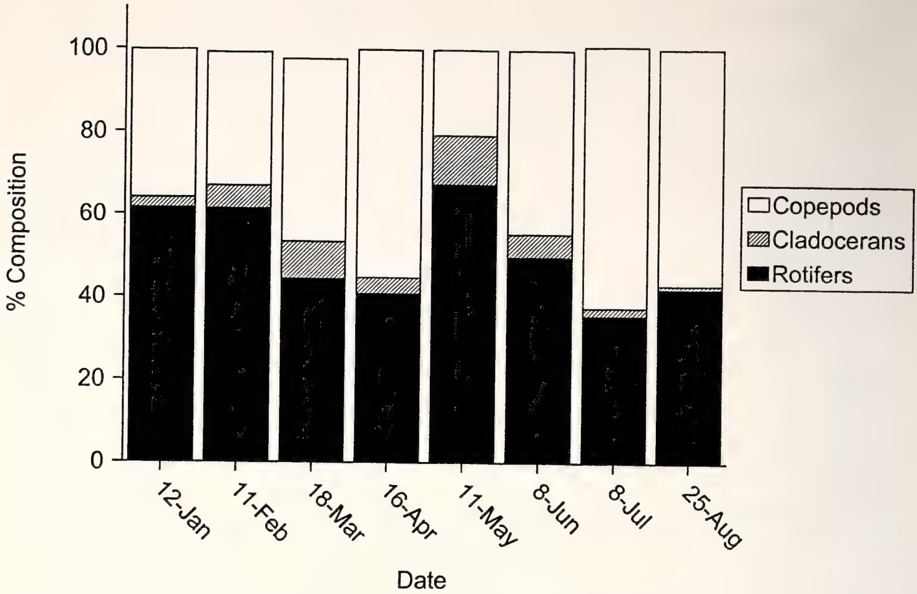

FIG. 2. Percent composition by classification of zooplankton in monthly samples at Lake Wauberg, Florida from January–August, 1998. Organisms recorded as unidentified "other" were omitted from this graph; thus the combined percentage values do not equal 100% for any given month.

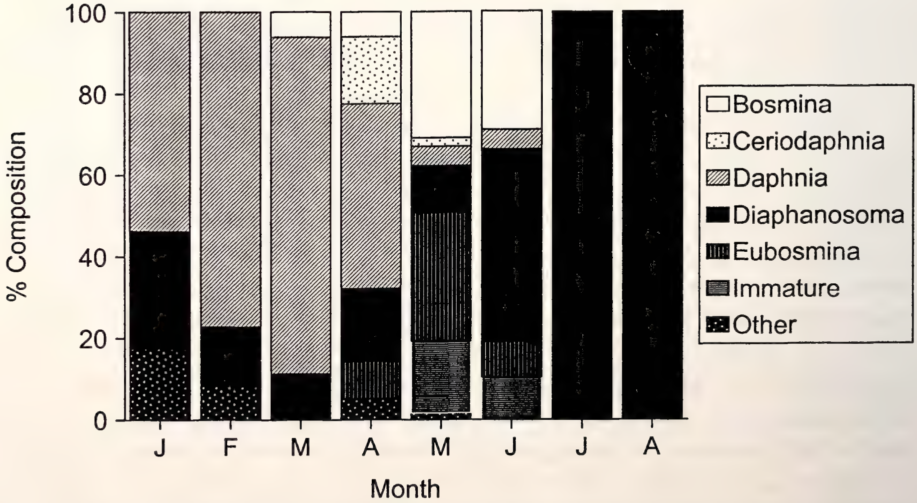

FIG. 3. Percent composition of the most common cladoceran genera for monthly samples at Lake Wauberg, Florida from January to August, 1998. "Other" corresponds to other cladoceran genera that were unidentifiable or were present in densities <5 indiv/L for all months sampled.

Peaks in abundance occurred in April and July (mean densities of 458 and 296 indiv/L, respectively) and were lowest in January and February (67 and 44 indiv/L) (Fig. 1). Copepods comprised the largest proportion of zooplankton in April (55%), July (63%) and August (57%) (Fig. 2). Nauplii dominated the copepod community in all samples comprising >70% of all copepods collected. Thus, nauplii abundance was responsible for the overall trend in copepod abundance. Calanoid copepods peaked in abundance in April (53 indiv/L) and cyclopoid copepods peaked in July (21 indiv/L).

Mean rotifer density varied among months (ANOVA, $P < 0.01$) with May having a significantly higher density than all other months except April ($P < 0.05$, Fig. 1). Rotifers dominated the zooplankton community in early spring (January and February) and again in May with their numbers comprising >60% of the total zooplankton community (Fig. 2). The most abundant rotifers were *Conochilus/Conochiloides* (grouped together) and *Brachionus* which dominated from January to May and from June to August, respectively. *Conochilus/Conochiloides* constituted >60% of the rotifers present in samples from January through March and >92% in April and May. *Conochilus/Conochiloides* abundance declined in June (14 indiv/L). Concurrently, *Brachionus* increased in abundance from 18 indiv/L in May to 214 indiv/L in June. *Hexarthra* and *Anuraeopsis* were found from July through August, whereas *Filinia, Kellicottia, Synchaeta,* and *Tetramastix* were either intermittently present or present at low densities throughout the study. *Asplanchna* peaked in abundance in January and June at 19 indiv/L, but otherwise was absent or present at low densities (<6 indiv/L). *Polyarthra, Keratella* and *Trichocerca* abundance peaked with densities of 20, 13, and 15 indiv/L, respectively. These peaks occurred in late spring (March and April) for *Polyarthra* and *Keratella,* respectively, and summer (July and August) for *Trichocerca.*

Zooplankton size structure—Mean cladoceran size varied among the months studied (ANOVA, $P < 0.01$). Mean length of cladocerans ranged from 0.30 mm in May to 0.52 mm in August (Fig. 4). This shift in mean size was due to a shift in species composition. In May, the two dominant cladocerans were *Bosmina* and *Eubosmina* which had a mean size of 0.27–0.28 mm, respectively. In April, *Daphnia* (mean = 0.51 mm), was most abundant, but in summer (June–August) *Diaphanosoma* (mean = 0.47 mm) was most abundant.

Mean length of copepods did not differ significantly among months in this study ($P = 0.20$, Fig. 4). Due to the dominance of nauplii, copepod size was nearly constant among months (range = 0.27–0.31 mm).

Rotifer size ranged from 0.06 to 0.15 mm and differed among months (ANOVA, $P < 0.01$). Mean rotifer size was lowest in April and May (0.08–0.09 mm) when *Conochilus/Conochiloides* (mean = 0.08 mm) comprised >92% of the rotifer community. Mean size increased in summer (June–August, Fig. 4) due to the dominance of *Brachionus* (mean = 0.12 mm)

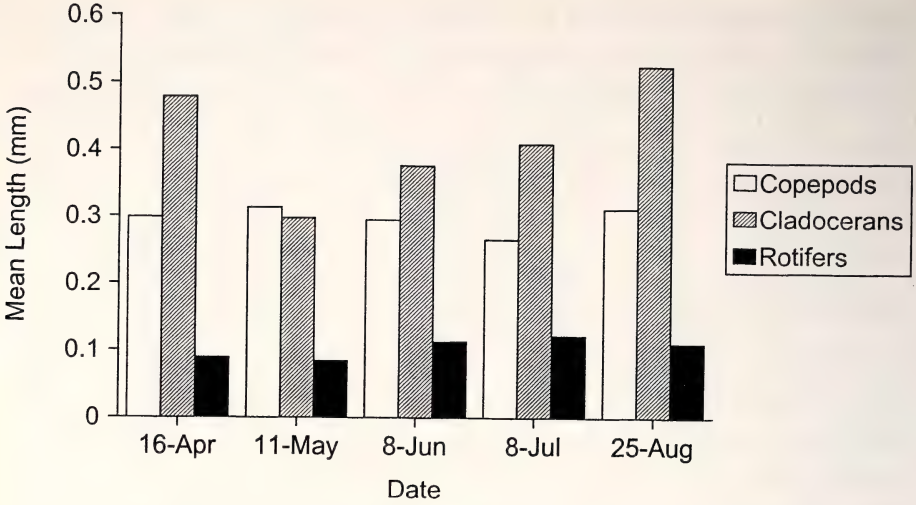

FIG. 4. Monthly mean length for zooplankton groups at Lake Wauberg, Florida from January to August, 1998. Standard errors for mean length of copepods, cladocerans, and rotifers were 0.01–0.02 mm, 0.01–0.04 mm, and <0.01 mm, respectively.

and/or the presence of *Trichocerca* (mean = 0.10 mm) and *Asplanchna* (0.28 mm).

DISCUSSION—*Patterns of abundance—Cladocera*—Cladocerans increased in abundance through spring, followed by a decrease throughout the summer at Lake Wauberg. This pattern of increasing density during the spring has been linked to increasing water temperatures (Shireman and Martin, 1978). Hazlewood and Parker (1961) showed that temperature was correlated with the density of *Daphnia,* but not *Diaptomus* at Kepple Lake, Washington. Bays and Crisman (1983) also found that sexual reproduction of *Daphnia* in Florida lakes occurred in late spring and summer with adults decreasing to extremely low levels by late summer. As in this study, *Daphnia* peaked in abundance in spring (February, March) followed by a decline and subsequent disappearance by late summer (July, August). Furthermore, immature cladocerans were found in the May and June samples, which would seem to indicate high reproductive activity.

The most common cladocerans found in Lake Wauberg mirrored those reported for other Florida systems. Nordlie (1976) found the most abundant cladocerans were *Eubosmina tubicen, Daphnia ambigua,* and *Diaphanosoma brachyurum* in three central Florida lakes in 1965–1966. Beaver and Havens (1996) also reported the most common cladoceran found in Lake Okeechobee was *E. tubicen*; however, *Daphnia* was extremely rare. In Lake Wauberg, *Eubosmina* was only co-dominant with *Bosmina* in May and with *Diaphanasoma* in June, and ranked as the fourth most common cladoceran found during the study period. Unlike Lake Okeechobee (Beaver and Havens, 1996), *Daphnia* was the most abundant cladoceran in Lake Wauberg during the study period.

Shireman and Martin (1978) found that *Diaphanosoma* was the most abundant cladoceran in Lake Wales, Florida from May through August and that its highest density was reached in May followed by a decline through the summer. Our results correspond with Shireman and Martin (1978) as *Diaphanosoma* was the dominant cladoceran in Lake Wauberg from June–August. *Bosmina longirostris* dominated the cladoceran community in the 8 North-Central lakes investigated by Blancher (1984) in 1976–1977 with *Ceriodaphnia* and *D. brachyurum* also present in large numbers in the spring. *Ceriodaphnia* exhibited low densities (≤7 indiv/L) and *Bosmina* was co-dominant only in May in this study.

Blancher (1984) did not report *Eubosmina, Ceriodaphnia,* or *Diaphanosoma* in Lake Wauberg, which were all represented in at least a portion of our samples. However, zooplankton community composition may change from year to year due to such factors as chlorophyll *a* concentration, fish species composition and abundance, pH, and temperature (Wells, 1969; Patalas, 1972; Blancher, 1984; Brezonik et al., 1984; Guest et al., 1990; Miller et al., 1990; DeVries and Stein, 1992; Hambright and Hall, 1992; Bremigan and Stein, 1994; Masundire, 1994; Hessen et al., 1995; Beaver and Havens, 1996; Canfield and Jones, 1996). Blancher (1984) reported Lake Wauberg as having a pH of 6.5 and mean chlorophyll concentration of 37.3 μg/l, whereas Florida LAKEWATCH (1997) data found a pH of 7.9, and, during the study period, a mean monthly chlorophyll concentration ranging from 43—120 μg/l (unpublished LAKEWATCH data). These differences, in addition to possible differences in fish predation between years, may explain why we found additional taxa than Blancher (1984) in Lake Wauberg.

Copepoda—Patterns in copepod abundance at Lake Wauberg were compared with previous studies. Copepod abundance was highly variable but mean values were generally higher in spring and summer than in January or February. Shireman and Martin (1978) found that copepod density peaked in April and August. This pattern contradicts a study conducted by Pace and Orcutt (1981) which reported that nauplii abundance in Lake Oglethorpe, Georgia declined in spring and remained at low levels throughout the summer. Much like Lake Wauberg, calanoids in Lake Wales showed a slight peak in May while cyclopoids showed a peak in August (Shireman and Martin, 1978). Similarly, Blancher (1984) found that cyclopoid copepods were most abundant in late summer and fall at Lake Wauberg. DeVries and Stein (1992) found that crustacean zooplankton experienced a single peak in the spring, followed by a decline in summer. This was also true for our study.

It has been hypothesized that the abundance of crustacean zooplankton in Florida lakes is governed by predation and temperature (Blancher 1984). Fish predation can reduce or alter zooplankton communities (Wells, 1969;

Blancher, 1984; Guest et al., 1990; Miller et al., 1990; DeVries and Stein, 1992; Hambright and Hall, 1992; Masundire, 1994; Hessen et al., 1995; Taylor and Carter, 1997; Torres-Orozco and Zanatta, 1998). For example, DeVries and Stein (1992) found that predation by gizzard shad reduced crustacean zooplankton abundance and fecundity of cladocerans. This decline occurred in June within two weeks of peak larval gizzard shad density. Gizzard shad were also believed to decrease phytoplankton abundance, indirectly affecting zooplankton abundance. Guest and co-workers (1990), however, found that threadfin shad *D. petenense* suppressed a portion of the zooplankton community, but gizzard shad had no effect. Hessen and co-workers (1995) investigated 342 Norwegian lakes and found that although the biomass of cladocerans and calanoid copepods were poorly correlated with lake productivity and fish predation, there was a correlation with shifts in average size and species composition. They found that at low productivities, water chemistry was the main factor affecting the abundance and biomass of zooplankton species. At increasing lake productivities, however, fish predation became increasingly more important. Because Lake Wauberg is highly productive, fish predation may strongly influence the zooplankton community.

Rotifera—Rotifers dominated the zooplankton community in early spring (January–February) and May, but constituted only about 46% of the zooplankton for the entire study period. Rotifers were found to dominate zooplankton communities at other lakes and reservoirs (Nordlie, 1976; Blancher, 1984; Hayward and Van Den Avyle, 1986; Canfield and Jones, 1996). Unlike Spring Lake, Florida, where mean annual rotifer densities exceeded cladoceran densities (Billets and Osborne, 1985), Shireman and Martin (1978) found that cladocerans outnumbered rotifers whose abundances were low except in January, April and August in Lake Wales, Florida. Blancher (1984) reported that rotifers accounted for 78% of the annual zooplankton abundance of Lake Wauberg. Similarly, in this study, rotifers far outnumbered cladocerans which contributed <10 % to the zooplankton community during the eight months of the study and did not exceed 12% of the zooplankton community during any one month. Nordlie (1976) reported that Florida lakes with high rotifer concentrations relative to cladocerans have low oxygen levels in the hypolimnion and high densities of *Chaoborus* larvae. Rotifers may dominate these systems, in part, because they have the ability to exploit low oxygen environments that are avoided by most crustacean zooplankton (Pace and Orcutt, 1981). However, we measured dissolved oxygen profiles on several occasions through the summer at Lake Wauberg and anoxic conditions were not present in deep water (>3 m) (M. Allen, unpublished data).

Rotifer species composition in this study differed from some other Florida lakes. The most abundant rotifers found in Lake Okeechobee, another shallow hyper-eutrophic Florida lake, were *Keratella cochlearis, Polyarthra*

TABLE 2. Body length (mm) for copepods and cladocerans collected at Lake Wauberg in this study and those collected by Canfield and Jones (1996) for temperature lakes.

Group	Mean	
	This Study	Canfield and Jones (1996)
Copepoda		
Nauplii	0.20	0.18
Calanoid	0.70	0.75
Cyclopoid	0.46	0.60
Cladocera		
Daphnia	0.51	0.83
Bosmina	0.27	0.29
Ceriodaphnia	0.31	0.42
Diaphanasoma	0.47	0.53

vulgaris and *Trichocerca multicrinis* (Beaver and Havens, 1996). In Spring Lake, Florida, the most abundant rotifer was *Hexarthra* spp. (Billets and Osborne, 1985), whereas the two most abundant rotifers in Lake Wales were *Keratella* spp. and *Conochilus unicornis* (Shireman and Martin, 1978). *Asplanchna priodonta* and *Polyarthra* spp. were also common in Lake Mize, and *Keratella* and *Tetramastix opoliensis* were co-dominants for parts of the year in Biven's Arm Lake (Nordlie, 1976). Newnan's Lake exhibited a variable pattern in rotifer abundance, but *Keratella* was most often present throughout the year although *Filinia longiesta,* when present, was often more abundant (Nordlie, 1976). In Lake Wauberg, *Brachionus* dominated the rotifer community in June and August and was co-dominant with *Conochilus/Conochiloides* in July. In all other months, *Conochilus/Conochiloides* was dominant. Other rotifers collected in this study were present in relatively low abundance (<20 indiv/L). The dominant rotifer in Lake Mize, an unproductive Florida lake, and Biven's Arm, which is productive, was *Brachionus havanaensis* (Nordlie, 1976). This correlates with a study conducted by Hessen and co-workers (1995) which found no evidence for classifying specific taxa as either "oligotrophic" or "eutrophic," but rather taxa are distributed among lakes of varying trophic states.

Zooplankton size structure—The mean size of cladocerans fluctuated in response to the abundance and size of genera dominating the community at a given time. The presence of larger-bodied cladocerans, such as *Daphnia* and *Diaphanosoma* caused an increase in mean size in April and through the summer, whereas the presence of *Bosmina* and *Eubosmina* resulted in a decrease in mean size in May.

Canfield and Jones (1996) measured different cladoceran genera in Midwestern reservoirs, including *Daphnia, Bosmina, Ceriodaphnia,* and *Diaphanosoma,* all of which were found in Lake Wauberg (Table 2). Mean sizes reported by the two studies did not vary greatly for the listed genera except for *Daphnia.* This difference supports the notion that smaller daphnids inhabit Florida lakes while larger-bodied species inhabit temperate lakes (Bays and Crisman, 1983). In addition to daphnids, Bays and Crisman (1983) reported that cladocerans inhabiting tropical lakes are often dominated by bosminids, moinids, *Ceriodaphnia,* and *Diaphanosoma.* This was generally true for cladocerans at Lake Wauberg which were dominated by bosminids, *Daphnia,* and *Diaphanosoma* at various times throughout the duration of the study. The average size of copepods measured in Lake Wauberg was similar to that reported by Canfield and Jones (1996) with the exception of cyclopoid copepods (Table 2). In general, smaller adult cyclopoid species were found in Lake Wauberg than for the more temperate lakes included in the Canfield and Jones (1996) study. This provides further evidence of latitudinal changes in the size of freshwater zooplankton.

The size range reported here for crustacean zooplankton at Lake Wauberg (0.27–0.32 mm) corresponds to the size range reported for crustaceans in a Ohio reservoir in summer (DeVries and Stein, 1992); however, the size range reported for two South Dakota lakes studied by Pope and Willis (1998) ranged from ~0.40 mm to ~0.80 mm. Although the Pope and Willis (1998) study corresponds to the accepted pattern of larger species in more temperate lakes, we advise caution with this generalization. For example, Lake Kariba, a tropical lake in southern Africa, was dominated by small zooplankton due to predation by the Lake Tanganyika sardine *Limnothrissa miodon* (Masundire, 1994), rather than due to its placement in a tropical region.

We found no studies that documented seasonal size shifts in rotifer size within the same body of water, nor did we find studies that compared rotifer size in temperate versus tropical or subtropical lakes.

Smaller zooplankton organisms in our samples were likely under-represented due to the mesh size of the plankton net used (Vannucci, 1968), whereas larger and more motile zooplankton organisms were likely under-represented due to gear avoidance (Clutter and Anruka, 1968). As such, mean size reported here for some of the smaller zooplankton genera may be overestimated, whereas mean size reported for the larger, more motile zooplankton genera may be underestimated.

CONCLUSIONS—Our results represent only an eight-month view of zooplankton dynamics through spring and summer at Lake Wauberg, which is important to consider when zooplankton dynamics can vary among years or within the same year due to fluctuations in the surrounding environment. Predation may be important in shaping the zooplankton community, although additional studies are needed to investigate factors affecting zooplankton community composition. Nevertheless, we found temporal changes in the zooplankton community within the year which may have important implications for fishes. Our results suggest that Lake Wauberg is typical of tropical systems in terms of zooplankton size structure, temporal dynamics, and species composition.

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AN EXPERIMENTAL ANALYSIS OF MAZE LEARNING IN THE WOLF SPIDER, *TROCHOSA PARTHENUS* (ARANEAE: LYCOSIDAE)

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ABSTRACT: *The maze learning ability of adult females of the wolf spider,* Trochosa parthenus *(Chamberlin) was investigated using a shock-avoidance protocol. Adult females demonstrated the ability to learn a relatively complex maze over an eight day training period. The number of blind alley errors decreased significantly, from a mean of 91.2 ± 9.4 on day 1 to 15.2 ± 3.2 on day 8. There was also a significant decrease in the amount of time required to run the maze (from 50.6 min to 10.4 min) over the same training period. This experiment represents the first demonstration of complex maze learning in lycosids. The adaptive significance of learning in spiders is also discussed.*

THE systematic study of learning (behavioral plasticity) in spiders and other arachnids has not received a great deal of attention compared to the amount of information available on insects (Alloway, 1972; Punzo, 1985, 1996). Various types of learning have been demonstrated in a few species of spiders including habituation, associative conditioning, shock-avoidance learning and acquired orientations (Laguelte, 1969; Lahue, 1973; Punzo, 1988). The various ways in which learning in insects might be adaptive has been the subject of much discussion (see reviews by Thorpe, 1963; Papaj and Lewis, 1993; Punzo, 1985), and there is no reason to assume that learning would not contribute to the overall fitness of spiders as well.

Traditionally, the behavior of arthropods has been considered to be instinctive, characterized by inflexible, genetically determined behavioral programs (Alcock, 1993). More recent analyses have indicated that many of these closed (instinctive) behavioral programs exhibit a greater degree of plasticity than previously thought (Curio, 1976; Punzo, 1985, 1995; Punzo and Garman, 1989). The ability of arthropods to modify their behavior based on past experience has led to a reassessment of the degree of behavioral plasticity exhibited by arthropods.

The purpose of the present study was to investigate the maze learning ability of the wolf spider, *Trochosa parthenus*. This spider is an active hunter, wandering over the ground surface and leaf litter in search of prey (Gertsch, 1979; Punzo, 1991). A maze learning experiment should serve as an ecologically relevant situation for an animal that could benefit from learning the

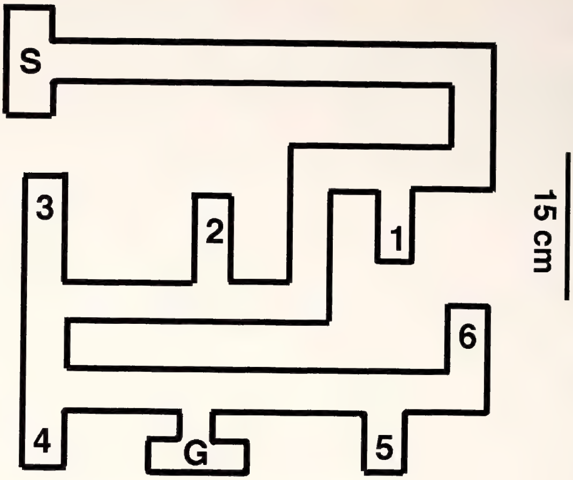

FIG. 1. Diagrammatic representation of the apparatus used for maze learning experiments in *Trochosa parthenus*. At the beginning of each trial, an individual spider was placed in the start box (S) and the number of blind alley errors made by each spider was recorded as it moved from S to the goal box (G).

most efficient foraging routes and locations where prey may be more abundant.

MATERIALS AND METHODS—The spiders used in all learning experiments were adult, non-gravid females raised as hatchlings from egg cases collected in the field. Egg cases were collected from females in Alachua Co., FL, during July and August, 1996. Spiderlings were raised to maturity on a diet consisting of small crickets (*Acheta* sp.), fruitflies (*Drosophila melanogaster*) and mealworms (*Tenebrio molitor*). Spiders were housed individually in plastic containers, placed in a Percival Model 80A environmental chamber, and maintained at 21° ± 1° C, 70% RH, and a 12L: 12D photoperiod regime. The mean body length (MBL = 7.88 mm) for all adult females used in these experiments ranged from 7.4–8.5 mm.

The maze used in these experiments had a floor plan modified from an earlier model described by Turner (1913). The maze is shown in Figure 1. It was constructed of opaque plexiglass and consisted of six blind alleys, a start box (S), and a goal box (G). The alleys were 3 cm in depth. The top of the maze was covered by a transparent glass plate. A 15-watt cool fluorescent lamp was placed directly over the center of the maze at a height of 25 cm, providing a source of illumination. The floor of the maze was constructed of wood and provided with an electrical copper grid through which a mild electric shock could be administered (square wave pulses of 10V amplitude at a frequency of 6 Hz). The strength of shock was chosen based on preliminary tests as well as values reported for insects (Kerkut et al., 1972).

An experimental group (EG) consisting of 20 spiders was subjected to maze learning trials. Each individal spider received 10 trials per day over an eight-day training period. Trials were terminated at this time due to the death of several spiders. At the beginning of each trial, a spider was placed in the start box for a period of one minute. The power source (Thornton Model 112 AGC stimulator) was turned on and the restraining panel between the start box (Fig. 1, S) and the main body of the maze was then removed manually, enabling the spider to enter the maze. The spider was allowed to traverse the maze and could avoid the shock upon entering the goal box (Fig. 1, G). The electrical grid in the goal box was covered with a thin piece of cardboard thereby insulating the spider from the shock. Each trial was terminated when the

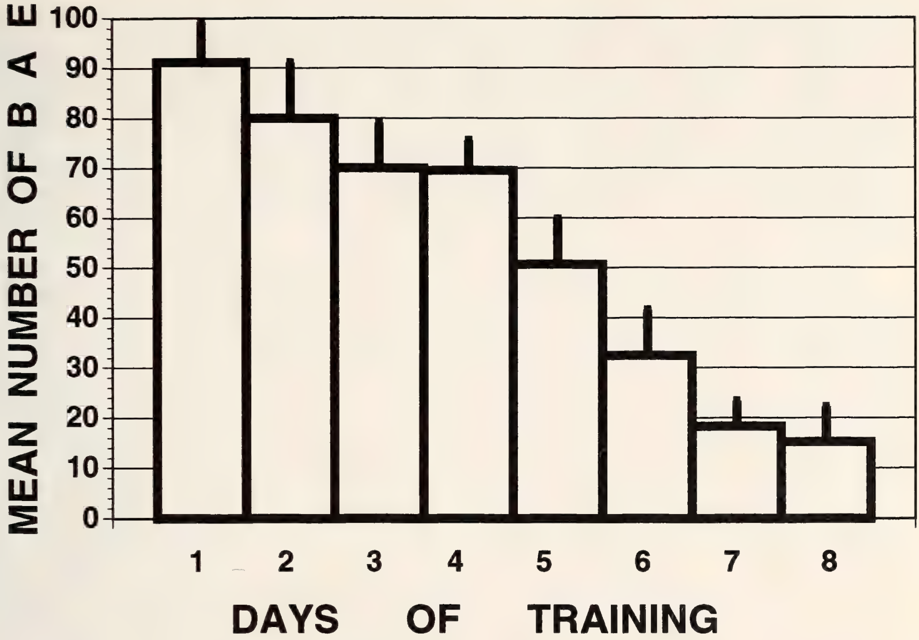

FIG. 2. Maze learning in *Trochosa parthenus*. Values represent the mean number of blind alley errors (BAE) for 20 adult female spiders. Each spider received 10 trials per day over an eight-day training period. Vertical lines represent $^+$ 1.0 S.D.

spider entered the goal box. The spider was allowed to remain in the goal box for 30 sec, then retrieved and placed back in the start box for 30 sec prior to the start of the next trial. After each trial, the floor of the maze was cleaned with a cotton swab containing a dilute (2%) solution of acetone to remove any odor cues or fragments of drag-line silk from the apparatus. Records were kept of the total number of blind alley errors (BAE) made by each spider for each trial over the eight day training period. An error was defined as such if more than one-half of the spider's body entered a blind alley. The time, in minutes, required to run the maze was also recorded for each trial.

A control group (CG, N = 20) was also tested in the maze. These spiders received an electrical shock even when they entered the goal box. This ensured that any differences between the performance of EG and CG spiders could not be attributed to differences in the general level of locomotor activity or to the experience of electrical shock (Schneirla, 1953; Punzo, 1980; Davey, 1989).

RESULTS—*Trochosa parthenus* clearly demonstrated the ability to learn this maze to avoid an electrical shock (Fig. 2). This is the first demonstration of trial-and-error learning for spiders in a relatively complex maze. The mean number of BAE decreased from 91.2 ± 9.4 SD on day 1 of training to 15.2 ± 3.2 on day 8. This represents a highly significant improvement in performance (t = 19.7, df = 19, $p < 0.01$). An ANOVA (Steele and Torrie, 1960) showed an overall significant effect of training days on performance (F = 57.4, $p < 0.01$) as well. In addition, the amount of time required to successfully navigate the maze decreased significantly over the 8-day training period (from a mean of 50.6 ± 7.6 min on day 1 to 10.4 ± 1.8 min on day 8) (t = 16.8, df = 19, $p < 0.01$). These spiders adapted very well to the confines of the maze and responded to the mild electric shock in a reliable way. It appears that *T. parthenus* are excellent subjects for this type of learning experiment. CG spiders showed no improvement in performance over the training period, due to the lack of reward (ability to avoid the shock) upon entering the goal box (99.3 BAE on day 1 vs. 103.2 on day 8).

DISCUSSION—The results of this study indicate that adult females performed quite well in a relatively complex maze. The ability to learn spatial features of their environment should facilitate capture of prey and location of suitable shelter sites. It is well known that many spiders and other arthropods exhibit relatively poor performance in various types of learning tests including mazes (Thorpe, 1963; Alloway, 1972; Lahue, 1973). As a result, there are few published papers on the learning abilities of many arthropods and other invertebrates. Therefore, it is important to identify those species that demonstrate an ability to solve a spatial learning problem such as a maze. It is clearly adaptive for an animal that actively searches for required resources such as food, water, nesting and ambush sites, and potential mates, to learn and remember the most efficient routes. A maze experiment is an excellent test to assess this type of behavior. It is not surprising, therefore, that arthropods which show a high degree of locomotor activity, mobility, and/or active pursuit of prey perform best in maze learning situations. This has been most clearly demonstrated for ants, cockroaches and thysanurans (Chauvin, 1947; Schneirla, 1953; Alloway, 1972; Punzo, 1980). In learning studies, it is imperative that researchers choose appropriate species and confront them with ecologically relevant learning tasks that take into consideration their biomechanical and sensory constraints.

Many species of lycosid spiders actively search for prey or regularly move to different locations (patches) to optimize prey availability (Gertsch, 1979; Hayes and Lockley, 1990). In northern and central Florida, *T. parthenus* is typically found on the ground and is associated with mesic habitats characterized by leaf litter and leaf mold. I have observed these spiders actively wandering over the surface of the ground in search of prey. The ability to learn more efficient foraging routes would reduce the amount of energy expended in searching for prey and would contribute to overall fitness.

Behavioral observations of *T. parthenus* within the maze indicate that maze learning occurs in distinct stages. During initial trials (Fig. 2, days 1–4), BAE are numerous and the spider spends a great deal of time exploring the bottom and sides of the runways with its pedipalps and legs. This is followed by a stage characterized by improved performance (days 5 and 6) where errors and exploratory activity decrease. Finally, a unified behavioral pattern is exhibited in which local responses become more organized and integrated into the correct route (days 7 and 8). Similar behavioral patterns have been reported for maze learning in ants (Schneirla, 1953).

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MYCORRHIZAL AND NITROGEN-FIXER ASSOCIATIONS WITH *CASUARINA* SPP. AND MYCORRHIZAL ASSOCIATIONS WITH *MELALEUCA QUINQUENERVIA* IN EVERGLADES NATIONAL PARK

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Abstract: Melaleuca quinquenervia *and* Casuarina *spp. invade sawgrass prairies low in occurrence of mycorrhizal infection and nitrogen-fixers. The presence of mycorrhizae associated with roots of* M. quinquenervia *and* Casuarina *spp. was investigated in three populations of each species in Everglades National Park, as was the presence of nitrogen-fixing nodules on roots of* Casuarina *spp.. Both* M. quinquenervia *and* Casuarina *spp. were found to be infected by vesicular-arbuscular mycorrhizal fungi (VAM), and* Casuarina *spp. roots from all sites were nodulated. VAM infection rates did not differ among* Casuarina *spp. stands, but did differ among* M. quinquenervia *stands.* Casuarina *spp. seedlings showed better growth on soils from the interior of the* Casuarina *spp. stand, than on soils from the surrounding sawgrass prairie. Mycorrhizal associations with* M. quinquenervia *and* Casuarina*'s ability to fix nitrogen could alter plant community composition in this region.*

Both mycorrhizae and nitrogen-fixers can influence community structure by changing patterns of plant establishment (Harly, 1970). Recently, mycorrhizal associations have been suggested to be important to the success of the establishment of wetland woody plants (Cantelmo, 1996; Stevens and Peterson, 1996; Rickerl et al., 1994; Khan, 1993; Keeley, 1980). We investigated whether two woody tree taxa, *Melaleuca quinquenervia* (Cav.) Blake, and *Casuarina* spp., with known mycorrhizal associations in Australia, where they are indigenous, were associated with mycorrhizae in habitats where they are exotics. These species are invading areas of sawgrass prairie in the Florida Everglades. Mature sawgrass (*Cladium jamaicense* Crantz) glades have a low incidence of mycorrhizal associations (Aziz et al., 1995) and few nitrogen fixers. Invasion by mycorrhizal and nitrogen fixing species may adversely affect future restoration efforts in the area (Johnson et al., 1992).

Casuarina spp. and *Melaleuca quinquenervia* were introduced to south Florida in the late 1800's. There are three species of *Casuarina* (Casuarinaceae; Australian Pine, She-Oak) in Everglades National Park, *C. glauca* Sieb. exk Spreng, *C. equisetifolia* L. ex J. R. and G. Forst., and *C. cunninghamiana* Miq.. It is difficult to distinguish among the species, which may hybridize, but within a stand all trees are likely to be the same species. In Florida, *Casuarina* spp. (hereafter referred to as *Casuarina*) becomes established in sawgrass glades, pinelands, and along sandy shores. *Casuarina* has mycorrhizal associations in its Australian habitat and is, also, known to be a nitrogen fixer (Khan, 1993). Nodulation is most likely caused by the presence of an actinomycete from the genus *Frankia. Melaleuca quinquenervia* (Myrtaceae; Paperbark Tree, Cajeput) (hereafter referred to as *Melaleuca*) is a wetland tree species that has become established in sawgrass glades, cypress domes, and wet pineland areas in south Florida (Ewel, 1986). Khan (1993) reported that *Melaleuca* is mycorrhizal under wet and dry conditions in its Australian habitat.

Casuarina and *Melaleuca* seedlings were difficult to establish in the field, and Casuarina seedlings rarely grew in the greenhouse. These difficulties prompted us to test whether there were mycorrhizal associations in both *Melaleuca* and *Casuarina,* and nitrogen-fixing associations in *Casuarina,* in Florida. We predicted that both species would have mycorrhizal associations, and that *Casuarina* roots would be infected with nitrogen-fixing bacteria. For *Melaleuca,* we examined both mature and young trees, predicting that mature trees would have higher levels of associations, because adult trees should be able to supply more oxygen to their roots, enhancing mycorrhizal associations (Jurgensen et al., 1997).

We further tested *Casuarina* establishment success on soils collected from within a stand, compared to soils collected from the surrounding sawgrass prairie. We hypothesized that *Casuarina* would have higher establishment occurrences growing on soils collected within the stand, assuming that mycorrhizae or other factors needed for regeneration success would be more likely to be present in soils from within the stand.

METHODS—*Casuarina* populations were sampled from three sites close to the Chekika camping area in the Everglades National Park in Florida in January 1997. C1 is located five miles south of the camping area, C2 two miles north of the camping area, and C3 two miles east of the camping area. All sites were stands of *Casuarina* surrounded by sawgrass prairie. There was little or no standing water in any of the *Casuarina* populations. Along a transect through the center of each stand, one root sample and one soil sample was collected from each of five randomly located points.

Melaleuca populations were sampled from three separate sites in January 1997. The M1 population is located on the eastern edge of Everglades National Park close to the *Casuarina* population C3. Trees grow in periphyton on pinnacle rock and in depressions in the rock. No standing water was present at the time of sampling. Roots of both older trees and saplings were buried in sediment. Population M2 is located in the northeast corner of the Park along the L 31 Canal, about 0.6 km south of Rt. 41. All trees sampled at this site were in standing water. Roots sampled from older trees were suspended in the water column. Root samples from sapling trees were buried in the sediment. Population M3 is located on the west side of Rt. 997 across from Thompson Park. Older trees' roots were sampled from a seasonally flooded root mat that was exposed at the time of sampling. Roots in this mat were exposed with no soil substrate around them. Sapling roots from this site were sampled from sediments fully submerged in standing water.

At each site, a transect was set parallel to the direction of water movement, through the

TABLE 1. Mean ± standard error for pH, nitrate, and ammonium levels of soils at three *Casuarina* stands. Five samples were analyzed from each site.

Site	pH	NO_3, ppm	NH_4, ppm
C1	7.52 ± 0.21	2.78 ± 0.60	2.54 ± 0.54
C2	7.36 ± 0.67	1.62 ± 0.13	2.30 ± 0.16
C3	7.56 ± 0.12	1.52 ± 0.30	5.78 ± 0.60

center of the *Melaleuca* stand. At five randomly selected points along this transect, one root and one soil sample was taken from an older tree. Root and soil samples were obtained from the closest sapling on a perpendicular to each point on the transect.

Soil and root samples of both *Melaleuca* and *Casuarina* were placed in labeled airtight bags and kept at 4° C for transport back to the laboratory. All samples were then frozen until they could be assayed. Root samples were rinsed over a 2 mm mesh screen, and then placed in a pan of water. Soil and organic matter were removed by agitating the roots. Fine roots were separated from lateral roots, wrapped in moist paper towels, and frozen until assayed. Roots were examined under a dissecting microscope for the presence of nitrogen-fixing *Frankia* nodules, for ectomycorrhizal structures, and for VAM, using the procedure outlined in Cantelmo and Ehrenfeld (1999). One hundred and fifty root intersections were observed from each root sample.

For *Casuarina,* variance in mycorrhizal association levels among sites were determined using one-way analysis of variance (ANOVA) (SAS, 1990). Due to the low levels of occurrence in *Melaleuca,* the presence of vesicles, arbuscules, and hyphal structures were grouped together to give a total count of VAM occurrence. W-tests for normality were performed on old and young trees for each population at each site. Levels of occurrence of associations between young and old trees were compared using a Kruskal-Wallis test (Kruskal and Wallis, 1952). Young and old trees were pooled within sites to compare levels of occurrence among sites.

Soil cores were thawed, air-dried and sent to the Soil Testing Lab at Rutgers University for analysis. A 1:1 mix with deionized water was used to obtain pH. The electrode was adjusted with pH 4 and 7 buffer solutions. Nitrate and ammonium measurements were obtained using a colorimetric method on an auto analyzer (Markus et al., 1985).

In March 1997, *Casuarina* seeds and soil samples were collected from within site C2, and soil samples were collected from outside site C2, at least 50 m from the edge of the tree stand. The soil samples were transported back to the greenhouse at Rutgers University in an ice chest. We set up 4 replicate trays each of interior and exterior soils and planted *Casuarina* seeds in these trays. Two months after seed germination, the height of 48 plants in each tray and the number of branches of each of 48 plants were measured. The data were analyzed using ANOVA (SAS, 1990).

RESULTS—*Casuarina*—Soil analysis demonstrated that C1 had the highest nitrate levels and C3 had the highest ammonium levels. The pH did not differ significantly among sites (Table 1).

No ectomycorrhizal structures were observed on the *Casuarina* roots, but *Casuarina* did contain VAM infection. Arbuscules were rarely found, but there was a wide range of occurrence of vesicles and hyphae. There were no significant differences in VAM infection among sites ($p = 0.478$). Nitrogen-fixing root nodules were present on *Casuarina* roots from all sites. *Casuarina* planted on soils from within the stand grew taller and had more branches than *Casuarina* seeds planted in soil from outside the stand (Table 2).

TABLE 2. Means ± standard errors for height and number of branches of *Casuarina* seedlings grown on soils from inside and outside a *Casuarina* stand. Sample size equaled 48 plants per treatment. F values and p values for the ANOVA show that seedlings grew better on soils from stand interiors.

	Interior Mean	Exterior Mean	F	p
Height	8.45 ± 0.26	6.94 ± 0.29	3.94	0.0003
# Branches	3.62 ± 0.41	1.83 ± 0.33	9.47	0.0027

Melaleuca—The soil analysis revealed that ammonium and nitrate levels were lower in M2 than in M1 or M3. M1 had the highest pH of the three populations (Table 3).

We found no ectomycorrhizal structures; however, we did find VAM associations. Arbuscules were rare and there was a wide range of occurrence of vesicles and hyphae. When total VAM mycorrhizal associations were compared between young and old trees at each site, there was no significant difference between groups. However, our data suggest older trees consistently have greater VAM mycorrhizal association than younger trees (Table 4). There are significant differences among sites as well, with the M1 site having significantly higher VAM mycorrhizal association than M2. M3 is intermediate between M1 and M2 in these fungal associations.

DISCUSSION—We found endomycorrhizae associated with *Casuarina* roots, but no ectomycorrhizae. This result differs from the findings of Khan (1993), who did find ectomycorrhizae on *Casuarina cunninghamiana* in Australian soils. However, he found that ectomycorrhizae did not penetrate into the roots, and we did not survey the soils in this study for the presence of ectomycorrhizal inoculum.

We found nodules on the *Casuarina* roots sampled. Nodulation has been observed on *Casuarina* at other locales (Khan, 1993; Deweda and Mansour, 1992; Dawson et al., 1989; Zhang and Turrey, 1985; Berg, 1983; Diem et al., 1983; Lechevalier, 1983). This association aids the host through nitrogen fixation, and occurrences of nodulation have been found to be aided by mycorrhizae (Russo, 1989; Badr and Moawad, 1988; Kucey and Bonetti, 1988). To understand the nutrient availability to *Casuarina,* as well as possible effects this may have on community dynamics, further studies are needed focusing on the relationship of nodulation and mycorrhizae.

TABLE 3. Mean ± standard error of pH, nitrate, and ammonium of soil at three *Melaleuca* spp. stands.

Site	pH	NO_3, ppm	NH_4, ppm
M1	7.75 ± 0.02	1.61 ± 0.12	5.23 ± 0.53
M2	7.41 ± 0.07	1.34 ± 0.06	3.75 ± 0.58
M3	7.52 ± 0.05	1.62 ± 0.08	5.26 ± 0.71

TABLE 4. Median and means ± standard error of mycorrhizal infection levels in three *Melaleuca quinquenervia* stands. P-values determined from a Kruskal-Wallis test on the difference of VAM mycorrhizal associations between young and old trees within sites demonstrate were not significant (ns).

Site	Tree Age	Median	Mean	p- value
M1	Old	0.486	0.384 ± 0.080	0.465 ns
M1	Young	0.206	0.286 ± 0.096	
M2	Old	0.013	0.021 ± 0.010	0.917 ns
M2	Young	0.006	0.098 ± 0.090	
M3	Old	0.186	0.219 ± 0.080	0.465 ns
M3	Young	0.006	0.175 ± 0.110	

Our observation of better seeding growth on soils from internal stands of Casuarina promotes many questions. It may support the importance of mycorrhizae, or of some other substance present in these soils, to seedling establishment. In the field, further studies should test whether established trees facilitate seedling growth within and at the edges of *Casuarina* stands, by changing the soil properties.

Khan (1993) found both endo- and ectomycorrhizal associations with *Melaleuca quinquenervia* in Australian soils. We found only endomycorrhizal associations with *Melaleuca* in southern Florida. More extensive studies of this plant in Florida may yield an understanding of these differences. Other populations of *Melaleuca* could have ectomycorrhizal associations given the appropriate hydrological conditions and sources of ectomycorrhizal fungi.

The relationship of more mycorrhizal associations with older *Melaleuca* trees may be influenced by the different hydrological regime old trees grow under compared to young trees, in populations M2 and M3. The subsurface sediments from which young roots were sampled are probably flooded year round and receive little oxygen. These conditions could hinder the establishment of mycorrhizae. It is also possible that older trees are better able to supply oxygen to their roots to support mycorrhizae than younger trees. M1 had drier, more aerated soils which may account for the increased mycorrhizal associations there compared to the other two populations (Khan, 1974; 1993). This effect may result in different inoculum potential at each site or differences in available phosphorus.

The existence of mycorrhizal associations in *Melaleuca* and *Casuarina* within the Park should be investigated further. Presence of mycorrhizae should be investigated in different seasons, as mycorrhizal associations can vary seasonally (Jurgensen et al., 1997). Mature sawgrass glades tend to have low levels of mycorrhizal association (Aziz et al., 1995), and this could limit the spread of *Melaleuca* and *Casuarina* populations. Conversely, efforts to restore sawgrass prairie could be hindered if these species have changed the fungal community in the soil, or changed nitrogen availability.

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AN APPROACH ON IMPROVING THE HEALTH OF HUMAN POPULATIONS

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ABSTRACT: *Increasing human population growth has put pressure on converting marginal soils to productive farmland. Since many soils are deficient in certain essential nutrient elements, slow-release, granular singular superphosphate fertilizers could be compounded containing adequate amounts of all elements needed not only for crops produced but also for people subsisting on these crops. If this were done, increased food supplies and healthier human populations should result.*

AN ancient folk-saying, "we are what we eat," is appropriate when we consider essential elements needed for good health in modern times. Twenty-two essential elements are required, but nine more whose essentiality is uncertain should be present in sufficient amounts according to some authorities (Kaim and Schwederski, 1996).

On 12 October 1999, the population of the world reached six billion (Wright, 1999). Since only 11% of the world's soils are fertile enough to have no serious limitations for agricultural use, intense pressure is placed on using less-productive soils. Drought is a major limitation for about 28% of land and mineral stress for about 23%. Many soils affected by drought are alkaline, while most affected by mineral stress are acidic (Foth and Ellis, 1997). With global warming, increasing El Niño and La Niña variations place even greater pressure on agricultural production (Palmer, 1998).

Fertility of deficient soils can be improved through use of fertilizers having appropriate amounts of essential elements for plant growth. Sixteen elements have been shown to be essential for most plants (Table 1). These are carbon, hydrogen, oxygen, nitrogen, phosphorus, potassium, sulfur, calcium and magnesium which are classed as macronutrients. Iron, manganese, copper, zinc, boron, molybdenum, and chlorine as the chloride are classed as micronutrients. Some plants like alfalfa need cobalt for nitrogen fixation, and some more primitive plants need other elements (Foth and Ellis, 1997). Seven additional elements are essential for humans—sodium, silicon, fluorine, iodine, selenium, cobalt and chromium. These elements could be classed as trace nutrients since they occur in the human body in the parts per million range (Table 1). Essentiality for nine more—bromine, lead, cadmium, tin, vanadium, arsenic, boron, nickel, and lithium—is uncertain (Table 1). Boron is essential for plants but its essentiality for humans is uncertain;

TABLE 1. Average elemental composition of a human body (adult, 70 kg)

Element	Mass (g)†	Daily needed allowance (mg)†	Element	Mass (g)†	Daily needed allowance (mg)†
Oxygen	45,500		Copper	0.11	1.5–3
Carbon	12,600		Aluminum**	0.10	
Hydrogen	7000		Lead*	0.08	
Nitrogen	2100		Antimony**	0.07	
Calcium	1050	800–1200	Cadmium*	0.03	
Phosphorus	700	400–600	Tin*	0.03	
Sulfur	175	5	Iodine	0.03	0.15
Potassium	140	2000– 5500	Manganese	0.02	2–5
Chlorine	105	3200	Vanadium*	0.02	
Sodium	105	1100–3300	Selenium	0.02	0.05–0.07
Magnesium	35	300–400	Barium**	0.02	
Iron	4.2	10–20	Arsenic*	0.01	
Zinc	2.3	15	Boron*	0.01	
Silicon	1.4		Nickel*	0.01	
Rubidium**	1.1		Chromium	0.005	0.05–0.2
Fluorine	0.8	1.5–4	Cobalt	0.003	0.2
Zirconium**	0.3		Molybdenum	<0.005	0.075–0.250
Bromine*	0.2		Lithium*	0.002	
Strontium**	0.14				

† Kaim and Schwederski, 1996
* Essentiality uncertain
** Not essential

however, it is included in at least one vitamin and elemental supplement, Centrum Silver®. Even though at least six more elements are found in the human body—rubidium, zirconium, strontium, aluminum, antimony, and barium (Table 1)—it is believed that they are not essential (Kaim and Schwederski, 1996).

Since most crops are used primarily, or through animal secondary sources, for humans consumption, all essential and uncertain-essential elements for humans should be available in the soil for plant growth. Many plants will take up small amounts of uncertain-essential and non-essential trace elements (Foth and Ellis, 1997) so that all possible elemental nutrients needed for humans could be provided for by appropriate crops.

Of the 22 essential nutrient elements and 9 uncertain-essential elements, there are a number that many people lack—calcium, magnesium, potassium, iron, selenium, and even arsenic are probably most important. Hypocalcemia is found among 45 to 54% of adult women (Berry, 1999). A shortage of calcium in later years may cause osteoporosis, arteriosclerosis, hypertension, neoplasia, senile dementia, polyneuropathy, and perhaps dementia-parkinsonism complex (Fujita, 1990; Chutkow, 1990). Hypomagnesemia is primarily confined to neuropsychiatric and cardiac systems. A shortage of magnesium and calcium gives rise to delirium, apathy, depression, personality changes, and irritability. This interplay coupled with a shortage of potassium gives rise to cardiac and neuromuscular problems (Brautbar et al., 1990). Men whose diets included higher levels of potassium and magnesium had fewer strokes and lower blood pressure (O'Neil, 1998). With deficiencies of calcium, magnesium, and potassium, coupled with excessive amounts of vanadium, the ion VO^{2+} may replace calcium and magnesium in the nervous system. This ion appears to be a factor in manic-depressive illness (Nielson, 1995; Goodwin and Jamison, 1990). Also with these deficiencies, non-essential rubidium may replace potassium causing manic episodes in rhesus monkeys and may affect humans as well (Fieve, 1989). In addition, if excessive amounts of lead, and/or cadmium, and/or aluminium are present, severe problems in the nervous systems, healing of injuries, and reproductive disorders may result (Kaim, and Schwederski, 1996; Perl, 1988; Greger, 1988).

Both iron deficiency (anemia) which is common in developing countries and excessive iron intake (coronary diseases) cause severe pathological problems (Kaim and Schwederski, 1996). Deficiencies of other elements are: zinc causes skin damage, stunted growth, retarded sexual maturation, and reduction in taste perception; copper, artery weakness, liver disorders, and secondary anemia; manganese, infertility, and impaired skeletal growth; molybdenum, tungsten, and vanadium, retardation of cellular growth, and propensity for caries; cobalt, pernicious anemia; nickel, growth depression, and dermatitis; chromium and vanadium, diabetes symptoms; silicon, disorders of skeletal growth; fluorine, dental caries; iodine, thyroid disorders, and retarded metabolism; selenium, muscular weakness (esp. cardiomyopathy); arsenic, impared growth in animals (Kaim and Schwederski, 1996).

Without doubt, selenium recently has become the most discussed essential nutrient element, where popular publications make it appear as a miracle cure against cancer and the effects of old age (Kaim and Schwederski, 1996). A deficiency in selenium also causes male sterility in domestic animals (Strauss, 1999; Ursini et. al, 1999). In addition, a severe lack of arsenic can lead to disorders in reproduction and growth of land-living animals (Nielsen, 1991; Davies, 1981; and Kaim and Schwederski, 1996). Both selenium and arsenic have a very small therapeutic range (Kaim and Schwederski, 1996).

Strictly speaking, nutrient elements should be called essential only if their total absence in the human body causes severe, irreversible change. Table 1 shows the presence of non-negligible amounts of "nonessential" elements such as rubidium, zirconium, strontium, bromine, aluminum, and lithium in the human body. These elements are incorporated throughout the body with important essential elements. Elements such as arsenic, tin, lead, and cadmium which are known to be very toxic may have positive effects in trace amounts in the body. Note the case of arsenic above (Kaim and Schwederski, 1996), and that lead congregates in hair and nails where it may act as a fungicide. Possibly a physiological—if not always essential—function may have developed for all naturally occurring elements during the evolution of life (Horovitz, 1988). It is apparent that interactions between elements and human health need further study.

METHODS—There are many different kinds of soil through-out the world. Each soil has a different effect on the availability of elemental nutrient elements—especially trace elements-during plant growth. In strongly acid soils, molybdenum availability is severally restricted, while iron and aluminum have reached toxic levels for plant growth. In alkaline soils, pH has become so high that most micro and trace elements are not available (Paquet and Clauer, 1997; Sposito, 1989; Foth and Ellis, 1997). The availability of macro-elements (also called primary and secondary elements), micro-elements, and trace elements is discussed below for a variety of these soils.

Clay-loam soil in semi-arid climate—During the 1940s, my family farmed a hard, red winter wheat called Kan Red^R on a 7,000 foot high mesa in the Colorado Plateau Country of southeastern Utah. Mesas on this part of the plateau are well drained and have little alkalinity. The soil is very red and very fertile. This is the result of heavily mineralized red dust blown in each spring from the Permian red-bed siltstones of southern Utah and northern Arizona, where it is mixed with clays in Cretaceous shales (Baars, 1972). These clays make up much of the deposits in Cretaceous seas where they mixed with clams and other sea shells. Sulfuric acid-fallout from a near-by chemical plant and carbonic acid from the combination of atmospheric water vapor and carbon dioxide liberates calcium and other essential elements in this soil for use as fertilizer.

After annually harvesting a wheat crop in August, we grazed cattle, horses, sheep, and pigs on the quickly-sprouting "volunteer" wheat fields. In May of the following year we ploughed under the green manure wheat crop and animal waste manure and urine to further enrich the soil. Ploughed fields were left rough to trap and conserve moisture from summer thunderstorms, then harrowed and planted for another crop in late August for another crop of winter wheat. By summer-fallowing our fields this way, we got two years' moisture to produce one bountiful wheat crop. No synthetic inorganic fertilizers were needed. Please note that in 1996, our ranch had less than 6 inches of precipitation; in 1997, an El Niño year, over 30 inches of precipitation; in 1998, an El Niño year, over 20 inches of precipitation; and in 1999 a La Niña year, less than 1 inch of precipitation the first 4 months, and more than 21 inches of precipitation during the summer months, to give a disastrous wheat crop and a bountiful pinto bean crop. So rainfall is still the most important "fertilizer" (Palmer, 1999).

Clay-loam soil with moderate rainfall—Most of the very productive soils of the world are of this type (Sposito, 1989). During the 1960's, I upgraded a low-fertility clay soil field at my home in northeastern Illinois. This area, exposed by glacial action, consisted of a potassium-fixed illitic clay soil which would not grow good grass. After removing weedy grass, I tilled into the soil a 12-12-12 NPK (12% nitrogen as N, 12% phosphorus as P_2O_5, 12% potassium as K_2O) granular fertilizer containing all plant essential microelements, a mixture of finely-ground dolomitic lime, and magnesium oxide. I raised an excellent garden plus very productive berry bushes and fruit trees. Where I had left a small strip bare of dolomitic lime and at another location a strip bare of magnesium oxide, I had only mediocre results. I learned later that magnesium deficiencies were common in high potassium-fixed clay soils, high acid soils, sandy soils, and alkaline soils containing large amounts of gypsum (Wilkinson et al., 1990).

Silica-sand soil—These occur in Florida and many other parts of the world. They result from long-term desilicification of smectite clays and other aluminosilicate minerals by humic and fulvic acid chelates to form kaolinite clay in areas such as the southeastern United States. This process occurs most readily in tropical or semi-tropical regions where there is much rain, high temperatures, and sufficient organic matter to form the chelates and carbon dioxide. At low concentrations the silica is present as monosilicic acid, $Si(OH)_4$ which forms a true solution with the chelates and is moved downstream (Tan, 1998; Thiry, 1997; Krauskopf, 1956) to areas such as Florida. When the organic chelates are destroyed by oxidation, the monosilicic acid polymerizes. Colder temperatures and the presence of aluminum ions or other ions in sea water or salt lakes will cause these polymers to coagulate into granules of silica sand (Tan 1998; Paton, 1978). Thus, Florida gains the precipitated silica sand, while left behind in Alabama and Georgia are moderately acid soils containing kaolinite clay, reddish goethite ($FeO(OH)$), and white bauxitic gibsite ($Al(OH)_3$).

Florida silica soils are very deficient in clays. Also organic humis oxidizes very quickly and summer rains wash away the essential elements. After I had spent some time as Manager of Research and Development for C F Industries Inc., I became an independent chemist and consultant where I developed a slow-release fertilizer that contained in each granule all of the essential elements that are needed in plants (Palmer, 1979). This fertilizer was made by treating flocculated phosphatic-clay waste slime with sulfuric acid. This slime contained magnesium and calcium smectites (montmorillonites) along with finely divided calcium phosphate minerals and assayed 16% P_2O_5 (6.4% P). After the initial sulfuric acid reaction, microelements and potassium chloride were added and the mixture partially neutralized with ammonia. Then urea was added which was polymerized with formaldehyde, and the mixture granulated to give an 10–10–10 slow-release fertilizer. Test trials made with this fertilizer applied to Florida silica sand soil in my vegetable gardens were excellent. Further tests on lawn grass with a 23–5–5 slow-release formulation containing more polymerized urea were also excellent. Similar fertilizers made from dolomitic phosphate ores from Hardee County, Florida, were tested and gave good results (Palmer, 1979).

Moderate acid soil—Most of the soils of the southeastern United States are acidic requiring the application of high-calcium and dolomitic limes to reduce acidity. Liming decreases acidity while added gypsum reduces toxicity of aluminum ions. However, since kaolinite has such a low effective cation exchange capacity (ECEC) (Foth and Ellis, 1997), other means are needed to increase the level of essential elements (Palmer, 1988).

Lateritic acid soil—Throughout many tropical regions such as western Africa, most kaolinite has been converted to gibbsite containing the strongly acidic oxisols of aluminum and iron oxides. Twelve percent of the soils under cultivation in the world are of this type (Moffat, 1999). These lateritic soils need much high-calcium and dolomitic liming to reduce the acidity enough for certain specialized crops. Some work is being done to engineer plants to cope with acidic aluminum ions (Moffat, 1999). Even so, limes should be selected that do not contain arsenic or other toxic elements (Anon., 1999). Some gypsum, $CaSO_4 \cdot 2H_2O$, also is needed for improving the quality of these soils (Boulange et al., 1997).

During my visits to Ghana, I learned that only people, chickens, and snakes survive in the low tropical regions because of the tse tse fly. There is plenty of chicken waste available for fertilizer, but it is toxic to plants unless it is dried. Also, there are large deposits of phosphate ore in Ghana and Togo; however, they contain high levels of toxic cadmium and should not be used (Palmer, 1986) since processing results in 80% of the cadmium reporting to the phosphoric acid (Anon., 1978). Two countries, Denmark and the Netherlands, have required that high-cadmium ores must be blended with low-cadmium ones such as those from Florida and North Africa before making fertilizers. There has been publicity in these countries that cadmium was getting into the food chain causing mental problems (depression or manic episodes?) (Palmer, 1987). Some work has been done on chemically removing cadmium from the acid but was not very successful (Norris et al., 1992). Most phosphate ores do not have toxic levels of such elements with the exception of vanadiferous ores and those of Togo and Ghana (Anon., 1978). This area of Africa could be a market for ores from northern and eastern Africa, and from Florida whose high dolomitic phosphate ores could be the most useful.

Igneous acid soils—Going to the other extreme are soils that have resulted from relatively short weathering time of igneous minerals. Many regions in Africa such as Zimbabwe and

Zambia have partially weathered soils which contain a wide range of materials varying in both size and stability. These range from highly stable cations such as potassium and sodium through colloidal-sized mineral fragments, larger fragments, both of which consists of insoluble and unreactive minerals such as feldspars, and quartz (Paton, 1978).

Quartz sand and clays derived from feldspars are sorted as they are eroded and transported downslopes by running water. Sand is deposited first, then clay-sized particles. This sequence is seen in the Kafue Basin of Zambia and also has led to concentration of huge quartz sand deposits in the Congo and Kalahari Basins (Paton, 1978). Intermediate feldspar-quartz soils with little clay are found in higher elevations of Zambia and Zimbabwe. Most of these soils are acidic and deficient in most of the essential elements. In the poorer regions very little is done to improve the fertility of the soils; while in the more affluent areas, these soils are farmed using applications of granular triple superphosphate (GTSP), granular ammonium nitrate, and ground limestone. No additional essential elements are incorporated in the GTSP and summer rains wash much of the ammonium nitrate into streams and lakes (Palmer, 1987; Palmer 1997). Thus, both crops and humans subsisting on these crops are suffering from deficiencies in essential elements. Please note that in 1997, which was an El Niño year, Zimbabwe and surrounding countries had one of the driest years on record, and 1998, a La Niña year, was one of the wettest years on record (Palmer, 1999).

For these latter soils, I developed a fertilizer according to the following process: nitrogen containing materials such as chopped chicken feathers are agitated and digested with concentrated sulfuric acid initially at ambient temperature to liberate nitrogen nutrients. Crushed and ground animal and chicken bones are added, and followed by digestion of ground igneous carbonatite phosphate ores from central Africa (Chilembwe and Dorowa deposits) and southern Africa (Phaleborwa), to produce a mixture of nitrogen compounds, monocalcium phosphate, gypsum, and phosphoric acid containing some sulfuric and hydrofluoric acids. Ground potassium containing minerals such as feldspars, illitic clays, and muscovitic schists are now added. Hydrofluoric acid will help solubilize potassium. Then oxide minerals of micro and trace elements are added. Additions of smectitic clay with high effective cation exchange capacity (ECEC) ratios are useful to absorb these elements. The resulting mixture is treated with water slurry containing chicken manure and then with additional ground phosphate ore. Any available ammonium sulfate, nitrates, or urea can be added at this time. This step converts most of the monocalcium phosphoric acid to dicalcium phosphate and more phosphoric acid. This additional acid is neutralized by the added phosphate ore to give a cementatious material. The resulting mass is discharged into a heated pug-mill mixer to granulate the product fertilizer into dry, non-hygroscopic, slow-release, free-flowing granules that can be safely broadcast by farmers in their fields. Dolomitic phosphate ores as well as low-grade ones, and waste phosphate materials can be used in the process. This fertilizer, thus, can be custom formulated to meet the nutrient needs of crops grown by farmers, and that also will meet the nutrient requirements of the people that will use these crops for food.

Alkaline soil—Many soils of the world that were farmed extensively in the past are no longer cultivated because of excessive amounts of salts and high alkalinity. Large areas along the Tigris and Euphrates Rivers, and the Indus River are of this type. Other areas that are troubled by increasing salts and alkalinity are those along the Nile River in Egypt and the Sudan (Palmer, 1979), and those along the lower part of the Colorado River in the United States and Mexico.

Many of these soils can have their alkalinity reduced by using gypsum ($CaSO_4 \cdot 2H_2O$) (Mehlich and Tewari, 1974) and acidic fertiliziers containing essential elements. Since most alkalinity is caused by sodium carbonates and bicarbonates, the use of gypsum precipitates calcium carbonate leaving sodium sulfate, a neutral salt (Foth and Ellis, 1997). Precipitation of calcium carbonate also should coprecipitate arsenic (Anon., 1999), thus reducing the amount of arsenic that can be taken up by crops grown on these soils. Flooding of fields with discharge of the salt-containing waters into rivers, oceans, and seas should recover many of these soils for farming.

DISSCUSSION—The question arises: How nutritious are food crops raised on these soils?

In clay-loam soils of the semiarid, high mesa country, some mature wheat fields had small areas where wheat was three to six inches taller and had heads 30 to 50 percent bigger. These areas appeared to be where cattle had urinated thus providing more nitrogen which caused higher yields. Thus, we learned to occasionally farm pinto beans and alfalfa field to increase nitrogen levels. We ran a profitable farming operation without the aid of manufactured chemical fertilizers; however, the use of a nitrogen chemical fertilizer might have increased our yields by 30 to 50% and we didn't know what the availability of minor and trace elements was.

When World War II began, hog prices became profitable enabling us to fatten hogs on wheat and we raised 300 to 400 head a year. We developed our own Duroc-Hampshire hybrid-a white belted, red, bacon-type hog. We grazed the young hogs in herds of 100 to 150 head first on roots, browse, berries, pinyon nuts, acorns, wheat kernals lost in the harvesting process, and lots of red dirt. (Our hog herder was my 10-year old sister.) We supplemented this with meat from wild horses bought from the federal government as well as cattle and sheep that had died from bloat. We also found that the bones and skulls of these animals could be burned to supply a calcium phosphate ash. The hogs craved this ash especially when it was accompanied with a pile of slack lignitic coal containing red clay that they could chew on. When the hogs were about four months old, we put them into pens where they were fed cracked wheat in self-feeders. Our wheat had a high protein content and contained many elements needed by hogs for high growth rate, but since the pens were crowded there was much fighting and retarded growth. However, when we mixed a mineral nutrient supplement containing more essential elements with the wheat, the hogs became more contented and grew faster enabling us to ship them several weeks earlier than usual. Before the hogs were six months old, we had found eager buyers in Salt Lake City and Los Angeles. However, it is apparent that we needed more nitrogen, phosphate, and perhaps calcium and a number of microelements in our farmland for our hogs to have good physical and mental health (Palmer, 1999). Please note that during this time frame both my mother and brother suffered from depression—so we may have had essential element shortages, as well.

The 12-12-12 microelement fertilizer used on illitic clay-loam soils probably is the best commercial fertilizer on the market today. It consists of a granulated mixture of ammonium nitrate, urea, ammonium sulfate, and sulfuric acid blended with granular monocalcium/dicalcium phosphate (GTSP), granular potassium chloride, and granulated microelements—all the essential nutrient elements needed for plant life (Foth and Ellis, 1997). After application, though, microelement granules were so widely spaced that many plants could not get all essential elements. In addition, bacterial action could result in 30% of nitrogen value being lost to the atmosphere as nitrogen and nitrous oxide gases (Foth and Ellis, 1997). Summer rains also could wash soluble ammonium salts and urea into aquifers, streams and lakes. Finally my experimental gardening using this fertilizer demonstrated that more calcium and magnesium were needed than was available in the fertilizer showing need for improvement in its manufacture.

Since gypsum is needed in soil improvements, granular single superphosphate (GSSP) fertilizer containing mono and dicalcium phosphates, and gypsum, has become the preferred type. My experiments with Florida silica-sand soils have shown that macroelements and all micro and trace elements needed by plants and animals can be easily incorporated into a mixture. Urea then can be incorporated in the fertilizer by displacing hydrate water from gypsum and phosphate compounds and cross-linked with formaldehyde during granulation. This will result in a fertilizer with slow-release properties containing all known essential elements for both plants and animals.

Since this fertilizer is expensive and contains formaldehyde, further experimental work has shown that process changes and other binders can be used to manufacture slow-release fertilizers. One binder is a mixture of sulfuric acid-treated chopped chicken feathers and chicken manure; however, in Zimbabwe it is now economically feasible to feed chopped chicken feathers to chickens as a source of protein, and to feed chicken manure to cattle as a source of protein (Palmer, 1997). In countries where this is done, smectic-type clays, phosphatic clay slimes, or processed human waste sewage also can be used as binders for slow-release fertilizers. Use of human waste requires care since removal of its heavy metal contamination is difficult (Rhodes and Palmer, 1995).

The end product of crop production is food for people. Substandard soils may not have all essential elements needed for nurturing life. The missing essential elements can be incorporated easily into GSSP granules. However, another nine elements also may be essential for humans, so appropriate means are needed to include all 31 in fertilizers to meet the complete nutritional requirements of people for maximum physical and mental health. In the above mentioned processes, slow-release fertilizers can be produced to provide all essential nutrient elements needed by plants and humans which also minimizes loss of elements in streams, lakes, and aquifers. These fertilizers also reduce gypsum waste, and utilize low-grade phosphate ores.

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SEXUAL DIMORPHISM IN VESTIGIAL PELVIC BONES OF FLORIDA MANATEES (*TRICHECHUS MANATUS LATIROSTRIS*)—

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ABSTRACT: *Pelvic vestiges of 129 Florida manatees (*Trichechus manatus latirostris*) were examined to determine if size and gender could be determined from isolated bones. The distinctions are not apparent in smaller specimens but become more obvious with increases in total body length (TBL). Animals equal to or less than 150 cm have rudimentary pelvics that are composed of cartilage. At approximately 160 cm TBL, an ossification center develops within this cartilage. At approximately 200 cm TBL, the pelvics continue to form in bone but lack sexually dimorphic features. In animals larger than 225 cm TBL, the pelvic bones gradually develop dimorphic features. There is obvious sexual dimorphism among larger individuals, with male pelvic bones being more robust than female pelvic bones.*

THE majority of Florida manatee (*Trichechus manatus latirostris*) carcasses recovered in the southeastern United States are necropsied by staff from the Florida Marine Research Institute (Ackerman et al., 1995). Maximizing the information obtained from every carcass is highly desirable, particularly since the Florida manatee is an endangered species. Externally, a manatee's gender can be determined from differences in the position of the urogenital opening relative to the anus. Internally, the gross differences between male and female reproductive organs are used to determine gender. In badly decomposed carcasses, these and other soft tissue landmarks are destroyed, resulting in approximately 5% of recovered carcasses unidentifiable as to gender. It has been established that in some cetaceans (Kleinenberg et al., 1969; Berzin, 1972; Perrin, 1975; Rommel, 1990) and in the dugong, *Dugong dugon* (Domning, 1991), there is a demonstrable sexual dimorphism in the pelvic bones. This study was initiated to determine if there is sexual dimorphism in the manatee's pelvic vestiges (anatomical position illustrated in Fig. 1A).

MATERIALS AND METHODS—The pelvic vestiges of 65 male and 64 female manatee carcasses were collected for this study. The bones were dissected from the carcass during necropsy and placed in water to macerate. Following maceration, the remaining soft tissue was removed. The bones were then degreased in a weak solution (0.07 %) of ammonia and whitened in a weak solution (0.07 %) of hydrogen peroxide for approximately 72 h each. Finally, the bones were air-dried for approximately 96 h. Once the pelvic bones were dry, their weights were measured with an electronic balance to the nearest gram, and lengths and widths were measured with calipers to the nearest 0.1 mm. Length was measured along the bone's long axis from the proximal base to the distal tip, and width was measured perpendicular to the length (Fig. 1B). Each measurement was repeated twice, and the averages were used in the calculations and graphs. Graphs of pelvic weights, lengths, and widths were created using Sigma-Plot 4.0.

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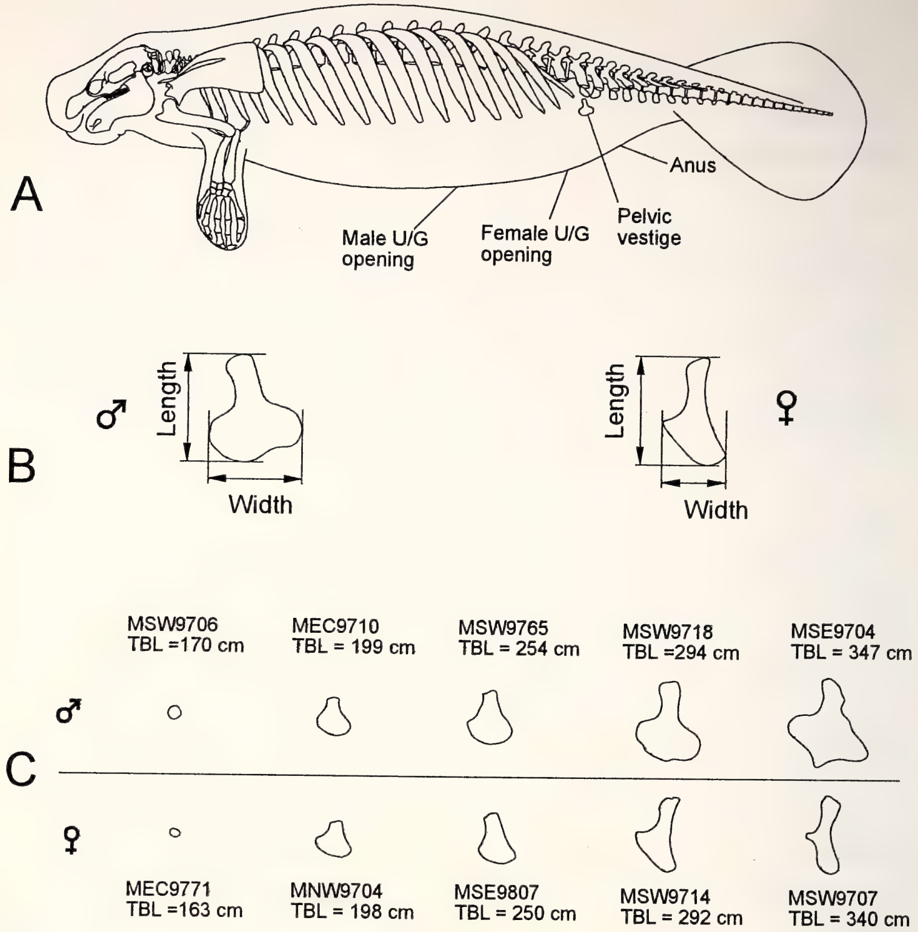

FIG. 1. (A) Left lateral schematic of a Florida manatee skeleton, illustrating the vestigial pelvic bones and their location in relation to other skeletal elements. The pelvic bones of both male and female manatees are located off the midline, caudal to the last rib and cranial to the anus. (B) Schematics of the left pelvic bone of male and female manatees. Length was measured along the bone's long axis from the proximal base to the distal tip, and width was measured perpendicular to the length. (C) A selection of distinct pelvic bones of male (top) and female (bottom) manatees of comparable total body length (TBL) showing the bones' change into sexually dimorphic skeletal elements.

RESULTS AND DISCUSSION—Male pelvic bones ranged in weight from 0.002 to 0.077 Kg. In contrast, female pelvic bones ranged in weight from 0.001 to 0.015 Kg. Male pelvic bones ranged in length from 1.44 to 12.16 cm and in width from 1.35 to 10.61 cm. In contrast, female pelvic bones ranged in length from 1.08 to 9.10 cm and in width from 0.94 to 6.39 cm.

Visual inspection of male and female pelvic bones shows several general trends (Fig. 1C). Small animals (≤150 cm total body length [TBL]) have rudimentary pelvics that are composed of cartilage. At approximately 160

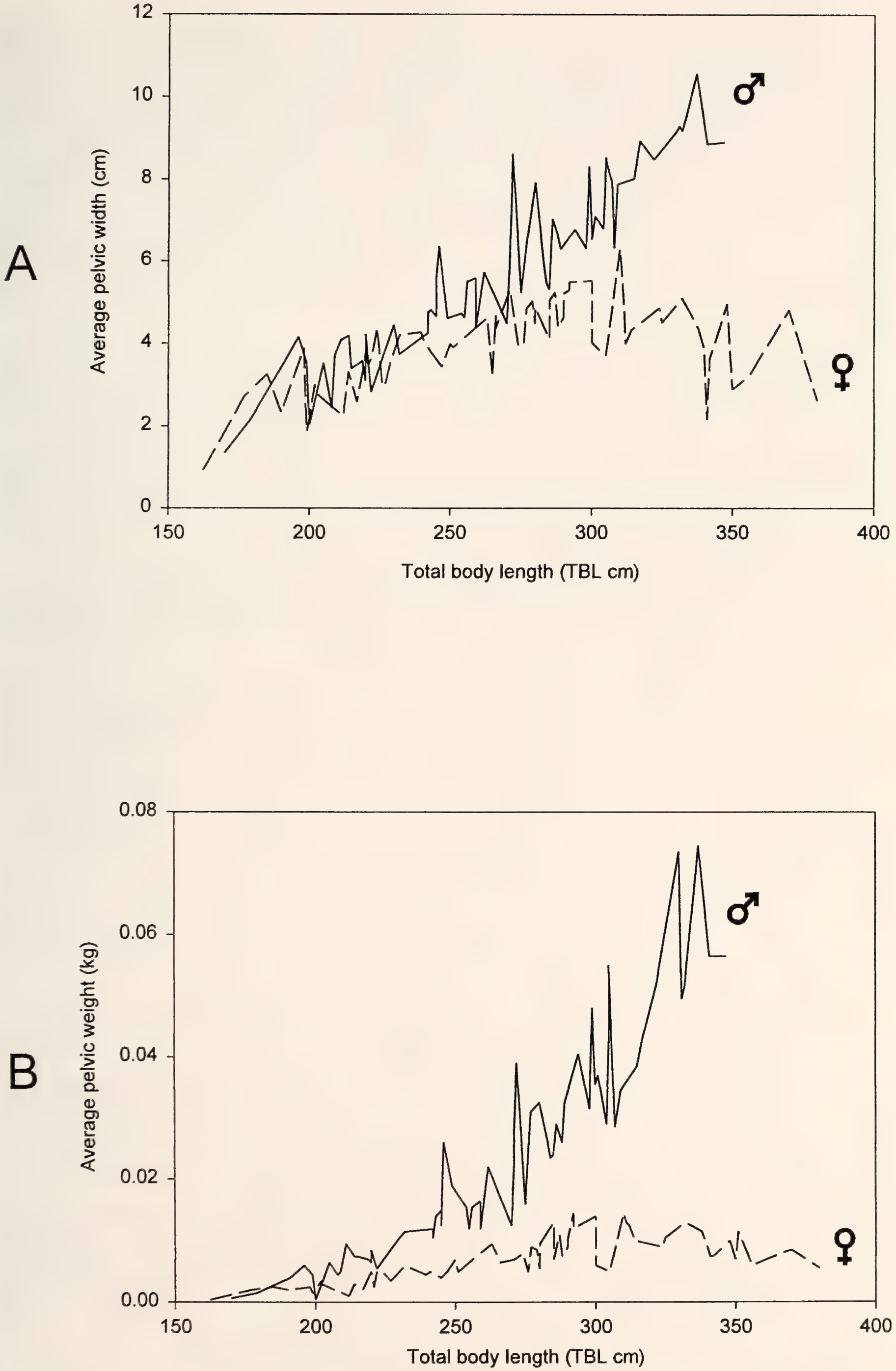

FIG. 2. (A) Pelvic bone width in relation to total body length for male and female manatees. (B) Pelvic bone weight in relation to total body length for male and female manatees.

cm TBL, an ossification center develops within this cartilage. These bony centers are very similar in males and females. At approximately 200 cm TBL, the pelvics continue to form in bone but lack sexually dimorphic features. In animals larger than 225 cm TBL, the pelvic bones gradually develop dimorphic features. For example, by 250 cm TBL, the pelvics of males tend to be broader, thicker and heavier than the pelvics of females. The differences in width and weight between male and female pelvic bones are shown graphically (Fig. 2A and 2B). The slopes for both width and weight are clearly different for males and females. The pelvic bones of male manatees increase in linear dimensions and in weight faster than the pelvic bones of female manatees do.

Manatees, like cetaceans, have no hind limbs and have only pelvic vestiges. These vestiges are embedded in the heavy musculature of the lumbocaudal region. The rectus abdominis and other muscles attach to the pelvics of both males and females of these aquatic mammals. The locomotory forces on the pelvic bones of males and females are similar and most likely would not influence sexual dimorphism.

Two aspects of sexual dimorphism in manatee pelvic bones need to be addressed: (1) Why do male pelvic bones become larger and heavier than female pelvic bones do? and (2) Why do the pelvic bones of females greater than 300 cm TBL decrease in size and weight?

According to Hernandez and co-workers (1995), male manatees reach sexual maturity at around 250 cm TBL. This life stage is marked by an increase in testosterone levels, which can cause bones to grow considerably in thickness. Additionally, the bones will continue to be remodeled by deposition and absorption so that they can properly support the mechanical forces imposed upon them (Guyton, 1976). The penial crura and their associated musculature are attached to the male pelvic bones (personal observation). The crural attachment sites are larger than the same general regions on the female pelvic bones are. These sites are relatively small in younger males but enlarge substantially in sexually mature males.

Decomposition hinders data gathering in all salvage programs; however, with the ability to gather data from skeletal remains, the decompositional state of soft tissues may no longer be as significant an issue. Our analyses show significant sexual dimorphism in the pelvic vestiges of the Florida manatee. With confidence, we can use the pelvic bones to determine gender of carcasses greater than 250 cm TBL, and with great confidence, we can determine gender of those greater than 300 cm TBL. The factors contributing to the sexual dimorphism are still under consideration, but the findings reported here are clearly a very important step in increasing our ability to gather information from each carcass collected.

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LATE PLEISTOCENE (RANCHOLABREAN) RECORDS OF THE HARVEST MOUSE (*REITHRODONTOMYS*) IN FLORIDA

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Abstract: *The late Pleistocene (Rancholabrean) fossil record of harvest mice in Florida consists of two species,* Reithrodontomys humulis *and* Reithrodontomys fulvescens. *The only extant species in the state is* R. humulis, *which occurs at four Rancholabrean localities. Today,* R. fulvescens *occurs only as far east as Mississippi, but is represented by a single mandible from Vero, Indian River County, Florida. This specimen was previously identified as* R. humulis *and later as* Peromyscus polionotus, *but dental and osteological characters permit confident allocation to* R. fulvescens. *This is the first synoptic description of fossil harvest mice from the Rancholabrean of Florida.*

The sparse paleontological record of harvest mice (genus *Reithrodontomys*) is only partly due to their diminutive size. In addition to being among the smallest nonvolant mammals in North and South America, they are rare even in modern environments (Howell, 1954; Kaye, 1959; Golley, 1962; Dunaway, 1968; Hall, 1981). The suggestion that *Reithrodontomys* may be more numerous than generally thought (Hamilton, 1943) is not supported by collections of either living or fossil samples. Early collections of fossil faunas missed the microvertebrates in the deposits, including remains of many bats, insectivorans, and rodents. With the development of screen washing as a common practice (Hibbard, 1949; McKenna, 1962; Cifelli, 1996), the microfauna that formerly seemed so rare now dominates many localities.

In spite of the screen washing techniques now employed, fossil harvest mice are still a rare find. The size of the screen mesh used is partly to blame for the lack of material; the commonly used 1/8 in (2.75 mm) and 1/16 in (1.4 mm) mesh screens are large enough for any isolated *Reithrodontomys* tooth to pass through. Accordingly, nearly all of the material reported here consists of the larger mandibles and associated teeth.

Materials and Methods—All fossils discussed are housed in the vertebrate paleontology collection of the Florida Museum of Natural History (FLMNH). The first mention of a fossil locality is followed parenthetically by the FLMNH site number. This locality number consists of two letters, representing the county for sites within Florida, and a three digit number assigned to a specific locality within the county. Specimens were measured with an optical micrometer to the nearest 0.01 mm. The illustration of the *Reithrodontomys fulvescens* dentition was drawn with a camera lucida attachment on a Wild binocular microscope. Recent specimens used for comparisons are housed in the FLMNH mammalogy collection and the Texas Memorial Museum Vertebrate Paleontology Laboratory. Collection abbreviations: TMM-M, Texas Memorial Museum, Vertebrate Paleontology Laboratory, recent osteology collection; UF, Florida Museum of Natural History, Vertebrate Paleontology Range; UF/FGS, Florida Geological Survey collection housed at the Florida Museum of Natural History. Dental terminology follows Reig (1977).

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SYSTEMATIC PALEONTOLOGY

RODENTIA Bowdich, 1821
MURIDAE Gray, 1821
SIGMODONTINAE Thomas, 1897
Reithrodontomys Giglioli, 1874
Reithrodontomys humulis (Audubon and Bachman, 1841)

Referred Florida Rancholabrean specimens—Arredondo 2A (AL009), Alachua County: UF 12548, right mandible with i1, m3; UF 56553, left mandible with i1, m2; UF 200202, right mandible with i1; Haile 11B (AL053), Alachua County: UF 200209, left mandible with i1; UF 200210, right mandible with i1, m3; UF 200211, left mandible with i1; UF 200212, right mandible with i1; UF 200213, right mandible with i1; UF 200214, right mandible with i1, m1; UF 200215, left maxilla with M1; Haile 13A (AL046), Alachua County: UF 13038a, right mandible with m2; UF 13038b, right mandible with i1, m2–3; UF 13038c, right mandible with i1, m1, m3; UF 13039, left mandible with i1; UF 13088, left mandible with i1, m1–2; UF 200217, left mandible with i1; UF 200218, left mandible with i1; UF 200219, right mandible with i1; UF 200220, right mandible with i1; UF 200221, right mandible with i1; UF 200222, right mandible with i1; Lecanto 2A (CI012), Citrus County: UF 118263, right mandible with i1; UF 118265, left edentulous mandible; UF 118266, left edentulous mandible.

Chronologic and geographic range—Fossil specimens are known from the earliest Irvingtonian (late Pliocene) through late Rancholabrean (late Pleistocene) of Florida and from the late Rancholabrean of California (Table 1). Recent eastern harvest mice occur in the southeastern United States, south to southern Florida, east to the Atlantic coast, north to southern Indiana, and west to eastern Texas and southeastern Oklahoma (Hall, 1981).

Diagnosis—Smallest species in the genus; molars brachyodont and lacking accessory cusps; upper molars with three roots and lower molars with two; major fold and second primary fold in M1–2 tend to coalesce, isolating anterior cusps; mandibular condyle more reduced than in other species of *Reithrodontomys,* and sits below level of coronoid, unlike other *Reithrodontomys;* anterior extent of masseteric scar situated directly under the anterior edge of the m1 alveolus, unlike other *Reithrodontomys* except *R. megalotis*; very pronounced labial cingulum on m1–2 distinct in the genus; concave anterolingual margin and convex anterolabial margin of m2–3; "C" shaped occlusal pattern on m3 (personal observation and modified from Howell, 1914; Hooper, 1952; Hall, 1981).

Reithrodontomys fulvescens Allen, 1894

Referred Florida Rancholabrean specimen—Vero, Stratum 2 (IR005), Indian River County, Florida: UF/FGS 1539, left mandible with i1-m3.

Chronologic and geographic range—Paleontologic records of the fulvous harvest mouse are confined to the Rancholabrean (late Pleistocene) and Holocene of Texas and the late Ran-

TABLE 1. Fossil occurrences of *Reithrodontomys humulis* and *R. Fulvescens*. Localities are followed by the source used for the chronologic placement of the site. Land mammal age terminology follows Morgan and Hulbert (1995).

Reithrodontomys humulis	
Inglis 1C, Citrus Co., FL; earliest Irvingtonian	Emslie, 1998
Haile 16A, Alachua Co., FL; late early Irvingtonian	Morgan and Hulbert, 1995
Coleman 2A, Sumter Co., FL; late Irvingtonian	Martin, 1974a
Haile 11B, Alachua Co., FL; late Rancholabrean	Emslie, 1998
Haile 13A, Alachua Co., FL; late Rancholabrean	Martin, 1978
Arredondo 2A, Alachua Co., FL; late Rancholabrean	Emslie, 1998
Lecanto 2A, Citrus Co., FL; late Rancholabrean	Emslie, 1998
Costeau Pit, Los Angeles Co., CA; late Rancholabrean	Miller, 1971
Reithrodontomys fulvescens	
Slaton Quarry, Lubbock Co., TX; late Rancholabrean	Hibbard, 1970
Easley Ranch, Foard Co., TX; late Rancholabrean	Dalquest, 1962
Vero, Stratum 2, Indian River Co., FL; late Rancholabrean	Weigel, 1962
Schultze Cave, Edwards Co., TX; late Rancholabrean/early Holocene	Dalquest et al., 1969
Hall's Cave, Kerr Co., TX; early Holocene	Roth, 1972; Toomey, 1993

cholabrean of Florida (Table 1). The modern distribution is south central United States (west to southern Arizona, north to southwest Missouri, east to western Mississippi) through Mexico, and south to Nicaragua (Hall, 1981).

Diagnosis—Moderate sized *Reithrodontomys* with average size larger than any other North American species except *R. hirsutus* and smaller than all South American species; mental foramen more lateral than other *Reithrodontomys* except *R. hirsutus* and more ventral than in *Peromyscus*; coronoid process short as in other members of the genus, but rounded unlike other *Reithrodontomys* except *R. hirsutus*; molars brachyodont; lower molars with two roots and lacking mesostylid, mesolophid, ectostylid, and ectolophid; reduced labial cingulum; slight anterolabial cingulum; posterostylid present on m2; "S"-shaped occlusal pattern on m3 rather than the "C"-shape of other *Reithrodontomys* except *R. hirsutus*; m3 relatively more elongate than in other *Reithrodontomys* except *R. hirsutus*. Lower incisors as in other *Reithrodontomys,* except *R. hirsutus* which is more anteroposteriorly elongate; masseteric scar situated more dorsally than in *R. hirsutus*; less enlarged capsular process than in *R. hirsutus*; coronoid process and condyle more inclined posteriorly than any other species in the genus (personal observation and modified from Howell, 1914; Hooper, 1952; Hall, 1981).

DISCUSSION—*Reithrodontomys fulvescens*—The only species of harvest mouse previously described from Florida, either fossil or recent, is the eastern harvest mouse, *Reithrodontomys humulis*. Florida's first published paleontologic record of *R. humulis,* a single mandible from Vero (UF/FGS 1539) reported by Simpson (1930), was subsequently reidentified as a beach mouse, *Peromyscus polionotus* by Bader (1959b). This specimen (Fig. 1) should instead be assigned to *Reithrodontomys fulvescens*. The more lateral placement of the mental foramen, the reduced labial cingulum, the elongate anterolabial cingulum on the m1, the distinct posterostylid on the m2, and, most importantly, the occlusal pattern of the m3 on UF/FGS 1539 distin-

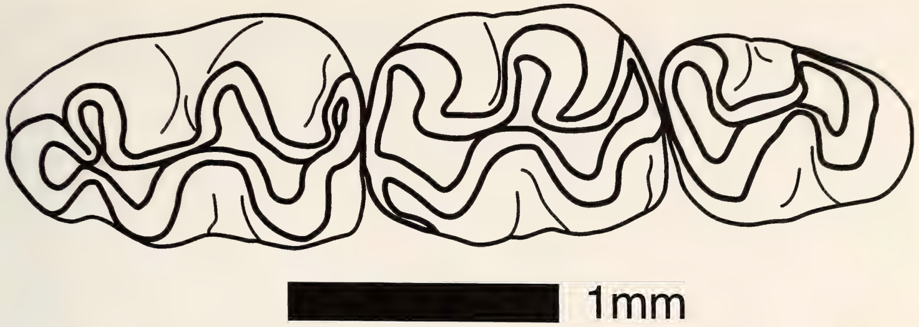

FIG. 1. Occlusal view of UF/FGS 1539 (*Reithrodontomys fulvescens* left m1–3 in mandible) from Vero, Florida. Anterior is toward the left and lingual is toward the top of the page.

guishes it from the eastern harvest mouse. *Reithrodontomys fulvescens* has an "S"-shaped occlusal pattern on the m3 created by the equal penetration of the hypoflexid and entoflexid. The m3 of *R. humulis* lacks the hypoflexid, creating a "C"-pattern. The taxonomic utility and importance of the m3 was discussed by Hooper (1952) in his revision of the harvest mice.

Compared to *Peromyscus polionotus, R. fulvescens* has a relatively greater mandibular depth. This robustness is reflected in the straighter ventral surface as compared to that of *Peromyscus* which has a much greater curvature, following the outline of the incisor. In *Reithrodontomys,* the posteroventral portion of the mandible twists nearly horizontally, with the inner margin raised. This leaves a depression in the ramus. *Peromyscus polionotus* has the mental foramen located higher compared to the position of the masseteric scar. The lack of accessory dental structures further argues for assignment to *Reithrodontomys,* though this evidence is not as convincing. Most *P. polionotus* m1s show a mesostylid (60% of 58 individuals), mesolophid (74%), and entosylid (72%), with the mesostylid (64%) and ectostylid (74%) of m2s similarly predominant (Bader, 1959a). Finally, although Bader (1959b) reported that the Vero specimen falls within the range of dental measurements for *P. polionotus,* its m1–3 alveolar length of 3.00 mm lies slightly below the 3.1 to 3.7 mm range (mean = 3.3 mm; n = 50) of beach mice measured by Martin (1967).

The similarity in dental pattern of the Vero mandible to that of *Reithrodontomys fulvescens* was noted by Bader (1959b), but he specified three points supporting his decision to assign it to *P. polionotus.* Two of his characters, the connection of the anteroconid to the protoconid and metaconid in the m1 and the lingual ridge of m2–3, are variable in expression both intraspecifically (personal observation) and within individuals (e.g. TMM-M 3385, *R. fulvescens*). Bader described the labial extension of the m3 hypoconid as relatively shorter in *R. fulvescens,* but this changes significantly with wear (Howell, 1914; Hooper, 1952). Finally, the "most unique feature is a very feebly developed anterolophid on the m3" (Bader, 1959b; p. 968), but I cannot discern this character and conclude it is lacking.

Reithrodontomys humulis—With only 11 specimens, Haile 13A represents Florida's largest Rancholabrean collection of *Reithrodontomys humulis.* Proportionately, this number is much more significant. Haile 13A contains only 12 mammalian taxa in its very small (~100 vertebrate specimens) collection. Haile 11B has approximately 1000 mammalian specimens representing 16 species. The other middle and late Pleistocene localities containing harvest mice have at least 30 species of mammals and thousands of specimens. Four mammalian species co-occur in all Florida Rancholabrean sites with harvest mice: *Blarina carolinensis, Scalopus aquaticus, Geomys pinetis,* and *Sigmodon hispidus.* These mammals are very widespread in the state as fossils, and therefore it is not possible to hypothesize an ecologic link between these taxa and *Reithrodontomys* based on fossil occurrences.

Table 2 presents the mean values for several measurements taken from Rancholabrean Florida harvest mice. There are too few teeth available to make any meaningful comparisons, but the m1–3 alveolar length was analyzed with a heteroscedastic two-sample student's t-test in order to assess the difference in the samples. The Arredondo 2A sample is significantly different from the Haile 13A and Lecanto 2A samples at a confidence level of 95%, and from the Haile 11B sample at a confidence level of 90%. The values of the Vero specimen reflect the greater elongation of *Reithrodontomys fulvescens.*

Other Reithrodontomys—Two additional Florida Rancholabrean sites not listed above contain *Reithrodontomys.* Riverview (HR003), Hardee County, contains a single isolated upper incisor, which is very distinctive due to its small size and deeply grooved lateral surface. The occurrence of "*Reithrodontomys* cf. *humulis*" (Karrow et al., 1996) at Oldsmar 1 (PI005), Pinellas County is also based on a single upper incisor. The presence of more than one type of harvest mouse in the deposits of Florida, however, precludes specific assignment. The deposits at Warm Mineral Springs (SA006), Sarasota County include two fragmentary mandibles tentatively assigned to the genus. Previously published faunal lists included *Reithrodontomys* at Reddick 1A (MR008), Marion County (Webb, 1974). I did not find any harvest mouse remains in the UF collection of Reddick 1A.

Miller (1971) identified "*Reithrodontomys* cf. *humulis*" from southern California, hesitating in the taxonomic assignment only because of the substantial geographic range extension it presented. The adequate sample size he had available and the distinctiveness of the labial cingulum on m1–2 allow the fossils to confidently be referred *R. humulis.*

The sole published Irvingtonian occurrence of *R. humulis* is at Coleman 2A (Martin, 1974a). Subsequent to that work, excavation at a newly discovered early Irvingtonian site, Inglis 1C, produced a single *R. humulis* tooth

TABLE 2. Comparison of Rancholabrean *Reithrodontomys* from Florida. Abbreviations: Alv., alveolar; Arr., Arredondo; Lec., Lecanto.

	Haile 11B	Haile 13A	Arr. 2A	Lec. 2A	Vero
Alv. Length					
Mean	2.88	2.86	2.71	2.89	3.00
Range	2.63–3.12	2.72–2.97	2.67– 2.75	2.86–2.91	—
sd	0.17	0.09	0.03	0.02	—
n	6	11	3	3	1
m1 length					
Mean	1.24	1.25	—	—	1.21
Range	—	1.23–1.26	—	—	—
n	1	2	0	0	1
m1 width					
Mean	0.74	0.83	—	—	0.77
Range		0.82–0.83	—	—	—
n	1	2	0	0	1
m2 length					
Mean	—	0.95	0.85	—	1.08
Range	—	0.94–0.95	—	—	—
sd	—	0.01	—	—	—
n	0	3	1	0	1
m2 width					
Mean	—	0.79	0.75	—	0.71
Range	—	0.71–0.85		—	—
sd	—	0.03	—	—	—
n	0	3	1	0	1
m3 length					
Mean	0.58	0.59	0.59	—	0.71
Range	—	0.59–0.59	—	—	—
n	1	2	1	0	1
m3 width					
Mean	0.62	0.61	0.62	—	0.54
Range	—	0.60–0.62	—	—	—
n	1	2	1	0	1

co-occurring with a large population an extinct species of harvest mouse (Ruez, 1999). Haile 16A contains a large sample probably also referable to *R. humulis* (Ruez, 1999).

CONCLUSIONS—The Rancholabrean fossil record of Florida contains two species of *Reithrodontomys,* with all known specifically identifiable material listed in this study. The modern fauna of the state includes only *Reithrodontomys humulis,* lacking *R. fulvescens,* which now ranges only as far east as Mississippi. A single mandible representing *R. fulvescens* from Vero, Florida is the only fossil specimen of the species outside Texas.

The occurrence of *Reithrodontomys fulvescens* in the fossil record of Florida is of little surprise. In addition to serving as a refugium for eastern North American mammals during the ice ages, the relative dryness and more equable temperatur es of the Florida Plio-Pleistocene attracted other mammals of "western affinities" (Webb and Wilkins, 1984). The *Capromeryx, Lepus, Orthogeomys,* and *Baiomys* of the Florida Irvingtonian (Martin, 1974a; Webb, 1974; Ruez, 1999) and *Spermophilus, Thomomys,* and *Conepatus* from the Rancholabrean localities in the state (Simpson, 1928; Ray et al., 1963; Martin, 1974a, b; Martin, 1978) are best known from west of the Mississippi River.

It is not possible to draw different ecological interpretations of the Vero locality based on the occurrence of *R. fulvescens,* rather than *R. humulis.* The eastern harvest mouse is most abundant in grasslands that are in early stages of vegetational succession (Kaye, 1959; Golley, 1962; Dunaway, 1968). *Reithrodontomys fulvescens* may be found in a much wider range of habitats, including that preferred by *R. humulis,* from dry grass and cactus ecotones to moist grassland-forests (Hooper, 1952; Packard, 1968). The geographic ranges of the two species today overlap broadly in eastern Texas, eastern Oklahoma, Arkansas, Louisiana, and western Mississippi (Lowery, 1974; Hall, 1981; Davis and Schmidly, 1994), precluding any potential habitat differentiation.

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CONTENTS

Biogeography of Amphibians and Reptiles of the Sea Islands of Georgia .... Joshua Laerm, Nikole L. Castleberry, M. Alex Menzel, Robert A. Moulis, Gerald K. Williamson, John B. Jensen, Brad Winn, and Michael J. Harris 193

Prey Selection by a Maternity Colony of Big Brown Bats (*Eptesicus fuscus*) in the Southeastern United States .... Michael A. Menzel, Timothy C. Carter, Brent L. Mitchell, Loren R. Jablonowski, Brian R. Chapman, and Joshua Laerm 232

Biology and Ecology of *Rivulus marmoratus*: New Insights and a Review .... D. Scott Taylor 242

An Evaluation of Mercury Levels in Spotted Seatrout, *Cynoscion nebulosus*, in Tarpon Bay, J.N. "Ding" Darling Wildlife Refuge, Sanibel, Florida, with Reference to Previous Studies .... James V. Locascio and Paul J. Rudershausen 256

Observations on the Growth of White Vine (*Sarcostemma clausum*) in a Nutrient-Enriched Region of the Northern Florida Everglades ...... Stephen M. Smith, Patrick B. Garrett, Jennifer A. Leeds, Julie Brewer, and Paul V. McCormick 261

Acknowledgment of Reviewers 273

Erratum 273

Book Review 274

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Biological Sciences

BIOGEOGRAPHY OF AMPHIBIANS AND REPTILES OF THE SEA ISLANDS OF GEORGIA

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ABSTRACT: *A review of available amphibian and reptile distributional records for 14 of the Georgia Sea Islands indicates 70 species are represented on these islands. These include 17 anurans, 8 caudates, the alligator, 11 lizards, 23 snakes, and 11 turtles. Examination of the records of 17 archaeological sites on three islands indicates numerous species previously present on these islands but for which there is no contemporary documentation. As a group, the islands of Pleistocene origin have a higher species richness of amphibians and reptiles compared to younger Holocene islands. Regression analysis of species richness against island size is highly significant, but species richness regressed against distance from mainland and distance from nearest neighbor island indicated no significant relationships. Species richness was significantly related to qualitative assessments of the amount of study islands have received but not to qualitative assessments of human impact. Multiple stepwise analysis based on size and study improved significance and goodness of fit values for regressions. Although this paper represents the most detailed summary of the current knowledge of herpetofaunal distributions on the Georgia sea islands, our knowledge of the bioeography of the islands is far from complete.*

COASTAL Georgia includes a series of barrier islands of varying size, geological origin, and past (as well as present) land management practices

(Figure 1). These sea islands have been the subject of considerable ecological attention and analysis (see Johnson et al., 1974; Sandifer et al., 1980; Stalter and Odum, 1993 for extensive literature). Yet, only limited information is available regarding much of their terrestrial fauna. In particular, the amphibians and reptiles are poorly documented. Summary checklists are available for several of the islands. Notable among these is that of Johnson and co-workers (1974) summarizing the earliest records. Additional checklists and summaries are provided by Hillestad and co-workers (1975) and Shoop and Ruckdeschel (1986) for Cumberland and Little Cumberland islands; Anderson and co-workers (1976) and Schwab and Shelton (1981) for Jekyll Island; Martof (1963), Teal and Teal (1964), and Laerm and co-workers (1999) for Sapelo Island; Zweifel and Cole (1974) for St. Catherines Island; and Ringler (1977) for Ossabaw Island. Numerous additional notes on records of occurrence of numerous species on various islands are also available (see below). Gibbons and Coker (1978) and Sandifer and co-workers (1980), utilizing Johnson and co-workers (1974) and other previously published data, provided comparisons of species richness and composition of the amphibians and reptiles of selected Georgia islands to several of those from Virginia, North Carolina, and South Carolina. Although, many of these studies are now several decades old, the herpetofauna of the Georgia barrier islands remains poorly understood. While several of the islands have been the focus of considerable collection activity and study, other islands have not. Recently summarized data now provide the basis for a more comprehensive review and analysis of amphibians and reptiles of the Georgia sea islands.

MATERIALS AND METHODS—We reviewed amphibian and reptile distributional records for 14 of the Georgia sea islands based on published literature, museum voucher records documented by Williamson and Moulis (1994), updated museum records obtained subsequent to Williamson and Moulis (1994), new survey records, previously undocumented records provided us by competent authorities, and our own unpublished records. We summarized data for each of the islands and for all the islands by taxonomic group. In addition, we reviewed relevant literature, unpublished reports, and faunal records of vertebrate remains recovered at 17 archaeological sites on Georgia barrier islands. For the purposes of comparison between insular and mainland herpetofauna, we include as mainland species only those that are documented from the immediate coastal counties (Bryan, Camden, Chatham, Glynn, Liberty, and McIntosh) based upon literature and museum voucher records listed in Williamson and Moulis (1994). These data provide the basis for statistical comparisons between islands and analysis of area- and distance-species richness relationships using simple linear and multiple (stepwise) regression (SAS Institute Inc., 1990). Surface area of islands referred to in the text and Table 1 is based upon upland terrestrial habitat given by Johnson and co-workers (1974) and United States Fish and Wildlife Service data. Upland habitat includes beaches and dunes above mean high tide level, forested areas, pastures, and freshwater ponds and marshes. It does not include salt marshes. Distances between islands and mainland and islands and islands were measured directly from U.S.G.S. topographic maps. We examined area-species relationships based on untransformed data. We calculated linear regressions using 1) total combined amphibian and reptile species richness, 2) amphibians and reptiles separately, and 3) by taxonomic groupings at the ordinal level.

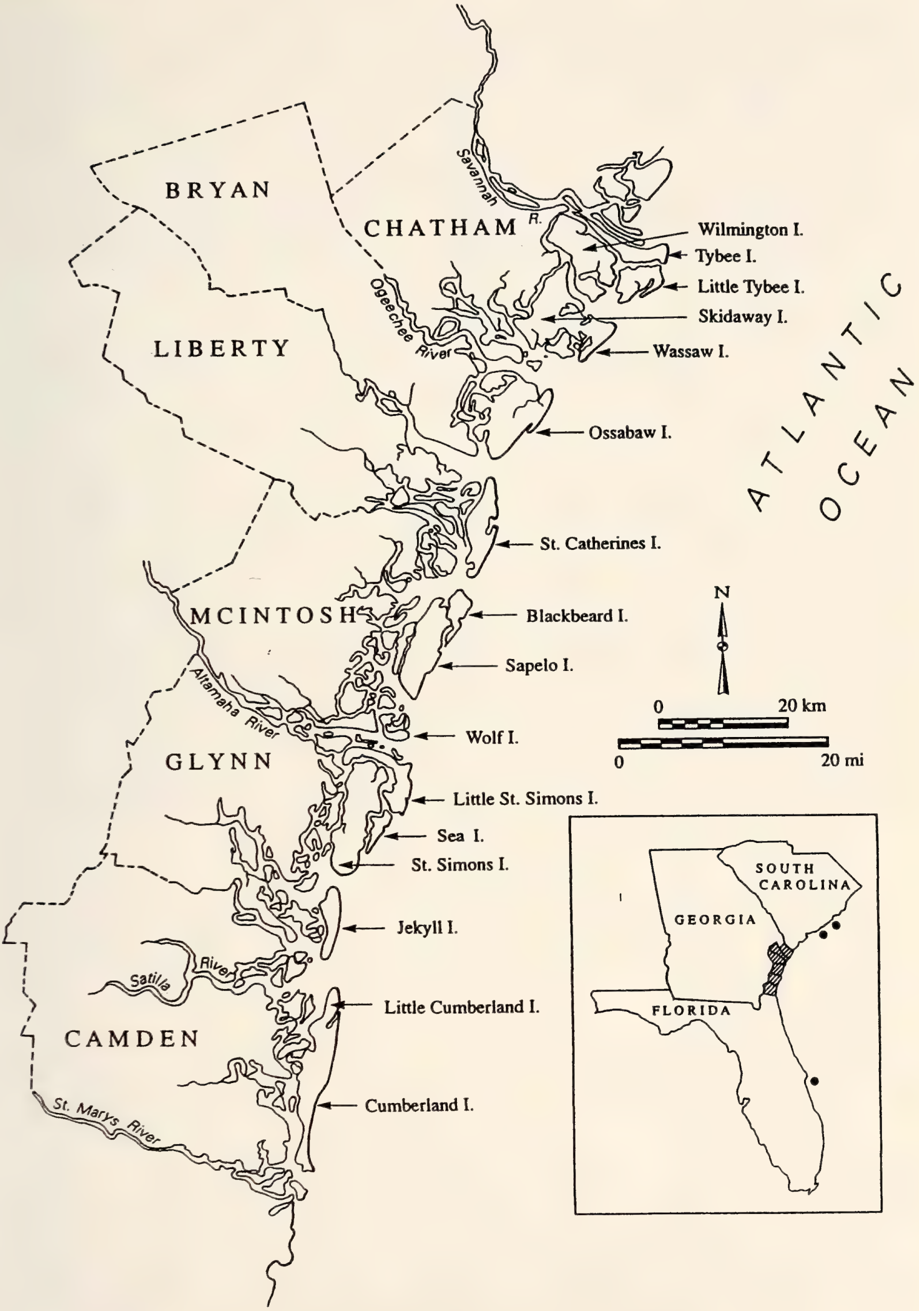

FIG. 1. The coastal counties and sea islands of Georgia. Map inset indicates approximate location (dark circles) of Kiawah and Capers islands, South Carolina and Merritt Island, Florida.

TABLE 1. List of amphibians and reptiles present in coastal counties of Georgia (Bryan, Camden, Chatham, Glynn, Liberty, and McIntosh) and on Sea Islands based on distributional records from Williamson and Moulis (1994), University of Georgia Museum of Natural History records not listed in Williamson and Moulis (1994), additional published records, and reliable observations. Numbers refer to sources described below. X = Unpublished museum records not included in Williamson and Moulis (1994); PO = Personal observation, cited in text; I = Introduced population; 1 = Ruckdeschel et al. (1982); 2 = Ringler (1977); 3 = Anderson et al. (1976); 4 = Kiviat (1982a–e); 5 = Mann and Kraemer (1979); 6 = Martof (1963); 7 = Hillestad et al. (1975); 8 = Williamson and Moulis (1994); 9 = Shoop and Ruckdeschel (1986); 10 = Seyle (1985a); 11 = Seyle (1985b); 12 = Johnson et al. (1974); 13 = Sandifer et al. (1980); 14 = Neill (1948); 15 = Tamarack and Doherty (1993); 16 = Zweifel and Cole (1974); 17 = Campbell (1996); 18 = Laerm et al. (1999); and 19 = Couper et al. (1996).

Island	Tybee	L Tybee	Wassaw	Ossa-baw	St Cath	Blkbrd	Sapelo	Wolf
Age	Holo	Holo	Holo	Pleist	Pleist	Holo	Pleist	Holo
Area of uplands (ha)	610	650	1015	4775	2915	1580	4415	120
Order Anura								
Family Bufonidae								
Bufo quercicus					8		6,8,12,13	
Bufo terrestris	12		8,12	2,8,12,13	8,12,13,1	8,12	6,8,12,13	
Family Hylidae								
Acris crepitans								
Acris gryllus								
Hyla avivoca								
Hyla chrysoscelis								
Hyla cinerea	PO		8,12	8,12,13	8,13,16	8	6,8,12,13	
Hyla femoralis					8,13,16		6,8,12,13	
Hyla gratiosa				8				
Hyla squirella	PO	PO	8,12	2,8,13	8,13,16	X	6,8,12,13	
Pseudacris brimleyi								
Pseudacris crucifer							X,8	
Pseudacris nigrita							8,12,13	
Pseudacris ocularis				2,18,13	8,13,16		6,8,12,13	
Pseudacris ornata								
Pseudacris feriarum								

TABLE 1. Continued.

Island Age Area of uplands (ha)	Tybee Holo 610	L Tybee Holo 650	Wassaw Holo 1015	Ossa-baw Pleist 4775	St Cath Pleist 2915	Blkbrd Holo 1580	Sapelo Pleist 4415	Wolf Holo 120
Family Ranidae								
Rana capito								
Rana catesbeiana				8				
Rana clamitans								
Rana grylio				8			6,8,12,13	
Rana heckscheri								
Rana sphenocephala			8,12	8	8,12,13,1	8,12	6,8,12,13	
Rana virgitipes								
Family Microhylidae								
Gastrophryne carolinensi	8			2,8,13	8,13,16	8	6,8,12,13	
Family Pelobatidae								
Scaphiophus holbrooki	PO			8	8,13,16		6,8,12,13	
Order Caudata								
Family Ambystomatidae								
Ambystoma cingulatum								
Ambystoma opacum								
Ambystoma talpoideum								
Ambystoma tigrinum								
Family Amphiumidae								
Amphiuma means					8,13,16		6,8,12,13	
Family Plethodontidae								
Desmognathus auriculatus								
Desmognathus fuscus								
Eurycea cirrigera				8				
Eurycea longicauda								
Eurycea quadridigitata				2,8,13	8,13,16			
Plethodon grobmani				2,8,13	8,13,16			

TABLE 1. Continued.

Island Age Area of uplands (ha)	Tybee Holo 610	L Tybee Holo 650	Wassaw Holo 1015	Ossa-baw Pleist 4775	St Cath Pleist 2915	Blkbrd Holo 1580	Sapelo Pleist 4415	Wolf Holo 120
Pseudotriton montanus								
Stereochilus marginatus								
Family Salamandridae								
Notophthalmus perstriatus								
Notophthalmus viridescens				8	8,13,16		6,8,12,13	
Family Sirenidae								
Pseudobranchus striatus								
Siren intermedia								
Siren lacertina				8				
Order Crocodylia								
Family Alligatoridae								
Alligator mississippiensi	PO	PO	8,12	2,12,13	12,13,16	8,12	6,8,12,13	
Order Squamata								
Family Anguidae								
Ophisaurus attenuatus								
Ophisaurus compressus							6,8,12,13	12,14
Ophisaurus mimicus								
Ophisaurus ventralis	8,12		8	2,8,13	8,13,16	8,12	6,8,12,13	
Family Polychridae								
Anolis carolinensis	8,12	PO	8,12	2,8,12,13	8,13,16	PO	6,8,12,13	
Anolis sagrei								
Family Phrynosomatidae								
Sceloporus undulatus							X,18	
Family Scincidae								
Eumeces egregius								
Eumeces fasciatus				8		8	8,12,13	
Eumeces inexpectatus			8,12	2,8,13	8,12,13,1	8	8,12,13	

TABLE 1. Continued.

Island	Tybee	L Tybee	Wassaw	Ossabaw	St Cath	Blkbrd	Sapelo	Wolf
Age	Holo	Holo	Holo	Pleist	Pleist	Holo	Pleist	Holo
Area of uplands (ha)	610	650	1015	4775	2915	1580	4415	120
Eumeces laticeps		PO		8,12,13	8,12,13,16		6,8,12,13	
Scincella lateralis			8,12	2,8,13	8,12,13,1	8	6,8,12,13	
Family Teiidae								
Cnemidophorus sexlinea	PO			2,8,13	8,13,16	12	6,8,12,13	
Family Colubridae								
Cemophora coccinea			8	2,8,12,13	8,13,16	PO	6,8,12,13	
Coluber constrictor	8	PO	8,12	2,8,12,13	8,12,13,1	8,12	6,8,12,13	
Diadophis punctatus								
Drymarchon corais								
Elaphe guttata			8		8,13,16		6,8,12,13	
Elaphe obsoleta	8,12	PO	8	8,12,13	8,13,16	12	6,8,12,13	
Farancia abacura				8				
Farancia erytrogramma							8	
Heterodon platyrhinos								
Heterodon simus								
Lampropeltis getula	8		8,12	2,8,12,13	8,13,15,1	8	6,8,12,13	
Lampropeltis triangulum								
Masticophis flagellum							6,8,12,13	
Nerodia erythrogaster								
Nerodia fasciatus			8	8	8,12,13,1	8,12	6,8,12,13	
Nerodia taxispilota								
Opheodrys aestivus			8	2,8,13	8,13,16	8,12	6,12,13	
Pituophis melanoleucus								
Regina rigida								
Rhadinaea flavilata								
Seminatrix pygaea							18	
Storeria dekayi			8			PO		

TABLE 1. Continued.

Island	Tybee	L Tybee	Wassaw	Ossabaw	St Cath	Blkbrd	Sapelo	Wolf
Age	Holo	Holo	Holo	Pleist	Pleist	Holo	Pleist	Holo
Area of uplands (ha)	610	650	1015	4775	2915	1580	4415	120
Storeria occipitomaculata							X,18	
Tantilla coronata								
Thamnophis sauritus	PO		8	2,8,13	8,13,16	8,12	6,8,12,13	
Thamnophis sirtalis				2,8,12,13	8,13,16	8,12	6,8,12,13	
Virginia striatula								
Virginia valeriae								
Family Elaphidae								
Micrurus fulvius				8				
Family Viperidae								
Agkistrodon contortix								
Agkistrodon piscivorus			8,12	8,12,13	8,13,16	8,12	6,8,12,13	
Crotalus adamanteus	8	PO	8	2,8,12,13	8,12,13,1	8,12	6,8,12,13	PO
Crotalus horridus					8,13,16		8	
Sisturus miliarius								
Order Testudines								
Family Chelydridae								
Chelydra serpentina				12,13		PO	6,12,13	
Family Emydidae								
Clemmys guttata								
Deirochelys reticularia			8	8,12,13	8,13,15		6,8,12,13	
Malaclemys terrapin	8	PO	8	8	8,16	PO	6,8,12	PO
Pseudemys concinna			PO					
Pseudemys floridana								
Pseudemys nelsoni								
Terrapene carolina							6,8,12,13	
Trachemys scripta			8,12	2,8,13	15,16	PO		

TABLE 1. Continued.

Island Age Area of uplands (ha)	Tybee Holo 610	L Tybee Holo 650	Wassaw Holo 1015	Ossa- baw Pleist 4775	St Cath Pleist 2915	Blkbrd Holo 1580	Sapelo Pleist 4415	Wolf Holo 120
Family Kinosternidae								
Kinosternon baurii								
Kinosternon subrubrum	PO		8	8	8,13,16	PO	6,8,12,13	
Sternotherus minor								
Sternotherus odoratus								
Family Testudinidae								
Gopherus polyphemus					I,16			
Family Trionychidae								
Apalone ferox								
Apalone spinifera								

TABLE 1. Continued. Extended.

Island	Sea	L St Sim	St Sim	Jekyll	L Cumb	Cumb
Age	Holo	Holo	Pleist	Pleist	Holo	Pleist
Area of uplands (ha)	930	485	4980	1780	650	6115
Order Anura						
Family Bufonidae						
Bufo quercicus						7,13
Bufo terrestris	8	PO	8	3,8,13	7,12,13	7,8,12,13
Family Hylidae						
Acris crepitans			8			
Acris gryllus			8			7,X,13
Hyla avivoca						
Hyla chrysoscelis						7,13
Hyla cinerea		PO	8	8,12,13	7,8,12,13	7,8,12,13
Hyla femoralis			8	3,8,13		7,8,13
Hyla gratiosa			8		7,13	7,13
Hyla squirella		PO	8	8,12,13	7,13	7,8,12,13
Pseudacris brimleyi						
Pseudacris crucifer			8			8,9
Pseudacris nigrita						7,13
Pseudacris ocularis			PO	3,8,13		7,13
Pseudacris ornata						
Pseudacris feriarum						
Family Ranidae						
Rana capito						
Rana catesbeiana				3,8,13		
Rana clamitans						
Rana grylio				4,8		7,8,13
Rana heckscheri						
Rana sphenocephala		PO	8	3,8,13	7,8,12,13	7,8,12,13
Rana virgitipes						

TABLE 1. Continued. Extended.

Island	Sea	L St Sim	St Sim	Jekyll	L Cumb	Cumb
Age	Holo	Holo	Pleist	Pleist	Holo	Pleist
Area of uplands (ha)	930	485	4980	1780	650	6115
Family Microhylidae						
Gastrophryne carolinensi		PO		3,8,13	7,12,13	7,8,12,13
Family Pelobatidae						
Scaphiophus holbrooki			8	4,8	7,12,13	7,8,12,13
Order Caudata						
Family Ambystomatidae						
Ambystoma cingulatum						
Ambystoma opacum						
Ambystoma talpoideum			8,11			7,13
Ambystoma tigrinum						
Family Amphiumidae						
Amphiuma means						8,9
Family Plethodontidae						
Desmognathus auriculatus						7,8,13
Desmognathus fuscus						
Eurycea cirrigera						
Eurycea longicauda						
Eurycea quadridigitata						7,13,X
Plethodon grobmani						
Pseudotriton montanus						
Stereochilus marginatus						
Family Salamandridae						
Notophthalmus perstriatus						
Notophthalmus viridescens					X	7,13
Family Sirenidae						
Pseudobranchus striatus						
Siren intermedia						

TABLE 1. Continued. Extended.

Island	Sea	L St Sim	St Sim	Jekyll	L Cumb	Cumb
Age	Holo	Holo	Pleist	Pleist	Holo	Pleist
Area of uplands (ha)	930	485	4980	1780	650	6115
Siren lacertina						
Order Crocodylia						
Family Alligatoridae						
Alligator mississippiensi		PO		PO	7,12,13	7,12,13
Order Squamata						
Family Anguidae						
Ophisaurus attenuatus						
Ophisaurus compressus		PO			7,13,X	7,13
Ophisaurus mimicus						
Ophisaurus ventralis		PO		3,8,13	7,12,13,X	7,8,13
Family Polychridae						
Anolis carolinensis		PO		12,13	7,12,13,X	7,8,12,13
Anolis sagrei			17			
Family Phrynosomatidae						
Sceloporus undulatus					12,13	7,8,12,13
Family Scincidae						
Eumeces egregius						8,9
Eumeces fasciatus						7,13
Eumeces inexpectatus				4,8	X	7,8,13
Eumeces laticeps		PO		8,12,13	7,12,13,X	7,8,12,13
Scincella lateralis	8	PO		8	7,13	7,8,12,13
Family Teiidae						
Cnemidophorus sexlinea		PO		4,8	7,12,13	7,8,12,13
Family Colubridae						
Cemophora coccinea				8,13	7,13,X	7,8,12,13
Coluber constrictor		PO	8	3,8,13	7,12,13,X	7,8,12,13
Diadophis punctatus			8			8,9

TABLE 1. Continued. Extended.

Island Age Area of uplands (ha)	Sea Holo 930	L St Sim Holo 485	St Sim Pleist 4980	Jekyll Pleist 1780	L Cumb Holo 650	Cumb Pleist 6115
Drymarchon corais						
Elaphe guttata	8		8	3,8,13	7,12,13,X	7,8,13
Elaphe obsoleta		PO	8	8,12,13	7,12,13,X	7,8,12,13
Farancia abacura			8			8,9
Farancia erytrogramma			8			
Heterodon platyrhinos			8			
Heterodon simus						
Lampropeltis getula	8	PO	8		7,12,13,X	7,8,12,13
Lampropeltis triangulum						7,8,13
Masticophis flagellum	8	PO		8	7,12,13,X	7,8,12,13
Nerodia erythrogaster						
Nerodia fasciatus				3,8,12,13	7,13	7,12,13
Nerodia taxispilota						
Opheodrys aestivus				4,8	7,12,13,X	8,12,13
Pituophis melanoleucus						
Regina rigida						
Rhadinaea flavilata					5,8	
Seminatrix pygaea						
Storeria dekayi						
Storeria occipitomaculata			8			8,9
Tantilla coronata						
Thamnophis sauritus			8	3,8,13	7,8,12,13	7,8,12,13
Thamnophis sirtalis			8	3,8,13	7,12,13,X	7,8,12,13
Virginia striatula						
Virginia valeriae						
Family Elaphidae						
Micrurus fulvius						

TABLE 1. Continued. Extended.

Island	Sea	L St Sim	St Sim	Jekyll	L Cumb	Cumb
Age	Holo	Holo	Pleist	Pleist	Holo	Pleist
Area of uplands (ha)	930	485	4980	1780	650	6115
Family Viperidae						
Agkistrodon contortix						
Agkistrodon piscivorus		PO	8	PO	7,12,13	7,8,12,13
Crotalus adamanteus		12	12	8	7,12,13	7,12,13,X
Crotalus horridus			8			7,13
Sisturus miliarius						
Order Testudines						
Family Chelydridae						
Chelydra serpentina		12			12	7,8,12,13
Family Emydidae						
Clemmys guttata						
Deirochelys reticularia				8		8,9
Malaclemys terrapin	8			8,12	7,X	7,8
Pseudemys concinna						
Pseudemys floridana						
Pseudemys nelsoni						
Terrapene carolina						8,9
Trachemys scripta						
Family Kinosternidae						7,8,12,13
Kinosternon baurii						7,13
Kinosternon subrubrum		PO	8		7,12,13,X	7,13
Sternotherus minor						
Sternotherus odoratus						
Family Testudinidae						
Gopherus polyphemus			8			7,12
Family Trionychidae						
Apalone ferox						7,13,X
Apalone spinifera						

We attempted to assess the significance of additional factors we hypothesized would impact insular species richness including the degree to which various islands have been surveyed or studied (with respect to amphibians and reptiles) and the degree to which the islands have been impacted by human activities. Judgments regarding these factors are subjective and difficult to quantify. However, we took mean values of independent rankings provided by three persons familiar with the barrier islands. Each island was ranked from 1 to 5 based on the ranker's knowledge of the degree to which that island's herpetofauna had been studied (1 = poorly, 5 = well). Each island was also ranked 1 to 5 based on the ranker's knowledge of the degree to which the islands have been impacted by anthropogenic factors (1 = low impact, 5 = high impact). Mean rankings were used as continuous independent variables in simple and multiple regression analysis along with area. We used G^2 log-likelihood ratio (SAS Institute Inc., 1990) to test difference in proportion of taxonomic groups between the mainland and geologic age of the barrier islands.

RESULTS AND DISCUSSION—*The Georgia sea islands in the regional perspective*—The sea islands comprise a complex of approximately 36 islands extending from South Island, South Carolina, to Cumberland Island, Georgia. These islands "stand as individual outliers of a broad wetland-estuarine system" (Lins, 1980). They are of mixed age; most are Holocene, but several of the larger are composed of both Pleistocene (Silver Bluff Formation) and Holocene sediments (Hoyt, 1967; 1968). The way these islands form is not known. Dune formation followed by flooding caused by glaciation during the Pleistocene, remains the most reasonable explanation (Hoyt, 1967; 1968; Johnson et al., 1974). Barrier islands are a common phenomenon along most of the eastern United States. To the north are the Mid-Atlantic Islands, of which there are approximately 70, extending from New Jersey and Maryland south to North Island, South Carolina. The Mid-Atlantic islands are composed of Pleistocene marine sediments and form part of the seaward edge of the Atlantic Coastal Plain. The Florida Atlantic Barrier Islands lie south of the Sea Islands of Georgia and include 22 islands extending from Amelia Island to Key Biscayne. The northern 12 (Amelia to Hutchinson) are of Holocene origin, while those to the south (Hutchinson to Key Biscayne) are of Pleistocene origin, and like the Mid-Atlantic islands, form an elongated beach continuum (Lins, 1980; Stalter and Odum, 1993).

Gibbons and Coker (1978) and Sandifer and co-workers (1980) described patterns of colonization of nine Mid-Atlantic and sea islands (one from Virginia, four from North Carolina, one from South Carolina, and three from Georgia) and found that amphibian and reptile species on islands were representative of those of the mainland; however, species richness on islands was dramatically lower than the mainland. In addition, they pointed out differences in colonization abilities between various groups. For example, lizards as a group are highly successful colonizers, while salamanders are not. Some comparisons of insular species community compositions between islands from Virginia to Georgia are possible, such as species area relationships described by Gibbons and Coker (1978); however, other comparisons or generalizations are difficult because the composition of the mainland herpetofaunal community available for island colonization in Virginia is very different from that of Georgia. Furthermore, the completeness of some of these faunal lists at the time of Gibbons and Coker (1978) was highly variable. However, given the apparent thoroughness of surveys on Kiawah Island and a more recent inventory for Capers Island, South Carolina (Gibbons and Harrison, 1981), as well as the availability of a checklist for Merritt Island, Florida, we contrast our discussion of the Georgia barrier islands to these in order to provide a regional perspective.

Herpetology on the Georgia Sea Islands—The seaward islands of coastal Georgia constitute a series of barrier islands, behind which lie a complex of variable-sized islands separated from each other and the mainland by salt marshes, rivers, and creeks of variable size (See Figure 1). With some notable exceptions (for example, Skidaway and Wilmington islands), the seaward barrier islands under discussion here are the only coastal islands large enough and of sufficient elevation to contain areas of upland habitat suitable for extensive colonization by many amphibians and reptiles. This is not to infer that numerous smaller islands do not support viable populations of amphibians and reptiles or that certain species of amphibians and reptiles do not inhabit marshes, creeks, and rivers. Certainly, larger islands, such as Skidaway and Wilmington, which lie behind the seaward islands, have been documented to contain numerous herpetofaunal species (Williamson and Moulis, 1994).

We acknowledge the occurrence of sea turtles on most of the islands, but do not include them in our discussion. *Caretta caretta* is known to use the coastal beaches during the summer nesting season (Hillestad et al., 1977; Richardson et al., 1980). This species is known to frequent the intercoastal waterway during warmer periods of the year as does *Lepidochelys kempii. Dermochelys coriacea* has been known to nest on Cumberland and Blackbeard islands (Ruckdeschel et al., 1982). During the 1996 nesting season, leatherbacks nested on Sea Island and Sapelo Island and attempted to nest on Blackbeard and St. Simons Island (Winn, 1996). In addition, Litwin (1981) reported a *Chelonia mydas* nesting on Jekyll Island.

The mainland herpetofauna of coastal Georgia includes 107 species with established populations. This includes the introduced brown anole, *Anolis sagrei,* which has only recently been documented as established on the coast in (at least) Camden and Glynn counties (Campbell and Hammontree, 1995; Campbell, 1996). Table 1 includes a listing of mainland and insular species by island with references for each taxon and island. Table 2 summarizes these data by taxonomic group (order).

Tybee Island is the northern-most of the Georgia barrier islands. It is of Holocene origin and contains approximately 610 hectares of uplands. It is accessible by highway and terminates in Savannah Beach, a heavily developed residential and recreational area. Despite its accessibility, there are few amphibian and reptile records (Johnson et al., 1974; Williamson and Moulis, 1994). Only two amphibian and seven terrestrial reptiles have been docu-

TABLE 2. Species richness of Georgia Sea Islands and coastal mainland by taxonomic group.

Group	Mainl	Tyb	L Ty	Wass	Oss	St C	Blbrd	Sap	Wolf	Sea	L SS	St S	Jekyll	L Cu	Cu
Anura	25	5	1	4	10	9	5	12	0	1	5	11	10	7	15
Caudata	18	0	0	0	5	4	0	2	0	0	0	1	0	1	5
Crocodylia	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1
Lacertilia	13	3	2	4	7	6	6	9	1	1	6	1	7	7	10
Serpentes	34	5	3	11	12	12	11	15	1	3	6	14	11	13	17
Testudinata	16	2	1	5	5	5	4	5	1	1	2	2	2	3	9
Total	107	16	8	25	40	37	27	44	3	6	20	29	31	32	57

mented by museum voucher records (Tables 1 and 2). There are seven additional observation records (Crawford, 1996) that we consider reliable: *Hyla cinerea, H. squirella, Scaphiopus holbrookii, Alligator mississippiensis, Cnemidophorus sexlineatus, Thamnophis sauritus,* and *Kinosternon subrubrum.* In addition, J. Crawford (1996) has observed *Gopherus polyphemus* on Tybee Island on four separate occasions. He opined that these were released pets brought onto the island. There is no evidence of an established *Gopherus* population on the island. The 16 species present represent 15% of the coastal mainland fauna.

Little Tybee Island is in close proximity to Tybee Island, separated only by Tybee Creek. Little Tybee is actually a conglomerate of small islands and hammocks, separated by sloughs and creeks. Upland areas encompass approximately 650 hectares. The island complex is of Holocene origin. There is no access from the mainland. No published or voucher records exist for terrestrial amphibians and reptiles of Little Tybee Island. Observational records attributable to J. Crawford (1996) include *H. squirella, A. mississippiensis, A. carolinensis, Eumeces laticeps, Coluber constrictor, Elaphe obsoleta, Crotalus adamanteus,* and *Malaclemys terrapin.* The eight species reported from Little Tybee Island represent 7% of the mainland fauna (Tables 1 and 2).

Wassaw Island is the largest of the Holocene islands with 1,015 hectares of uplands. It has no direct access to the mainland. It is administered as a National Wildlife Refuge, and access is restricted. Johnson and co-workers (1974) documented four anurans, three lizards, and three snakes. Since that time, salamanders have yet to be reported from the island, but four anurans, the alligator, four lizards, 11 snakes, and five turtles are now known (Tables 1 and 2). All are documented by voucher specimens (Williamson and Moulis, 1994), except an observation record of *Pseudemys concinna* (R. Moulis). The 25 species constitute 23% of the coastal fauna. Two additional species are not included in our records, *Sistrurus miliarius,* reported to have been killed by a previous refuge manager and more recently, *Agkistrodon contortrix,* observed crawling away from lumber transported from the mainland (R. Moulis). Although copperheads are common on Skidaway Island immediately to the west of Wassaw Island, it is likely the specimen observed was introduced. There is no evidence of established populations of either of the latter two species on Wassaw Island.

Ossabaw Island, encompassing approximately 4,775 hectares of uplands, is the third largest of the sea islands. It is of Pleistocene origin and has no direct access to the mainland. Johnson and co-workers (1974) reported anurans, the alligator, two lizards, seven snakes, and one turtle. Ringler (1977), apparently not familiar with Johnson and co-workers (1974) reported six amphibians and 14 reptiles, all supported by voucher documentation. With the addition of voucher records summarized by Williamson and Moulis (1994), 40 species are now documented: 10 anurans, five salamanders, the alligator, seven lizards, 12 snakes, and five turtles (Tables 1 and 2). These constitute 37.38% of the mainland fauna. The record of *Micrurus fulvius* on Ossabaw Island is the first for any of the Georgia barrier islands (see Table 1).

St. Catherines Island is of Pleistocene origin and includes approximately 2,915 hectares of uplands. The island is privately owned and access is limited. The checklists of Zweifel and Cole (1974, unpublished manuscript on file, St. Catherines Island) and Johnson and co-workers (1974) include 34 species. Subsequent published records (Tamarack and Doherty, 1993; Williamson and Moulis, 1994), brings the list to 37: nine anurans, four salamanders, the alligator, six lizards, 12 snakes, and five turtles, including the recently introduced *G. polyphemus* (Winn, 1996). We do not include the erroneous report of *Drymarchon corais* (Couper et al., 1996), which is a misidentified *C. constrictor* (Behler et al., 1997). All records are supported by voucher documentation. St. Catherines Island supports 35% of the mainland fauna. Five archaeological sites have been excavated on St. Catherines Island yielding herpetofaunal remains (see discussion below).

Blackbeard Island is a National Wildlife Refuge. Separated from the northeastern part of Sapelo Island by Blackbeard Creek, it is of Holocene origin and includes approximately 1580 hectares of uplands. Access is restricted. Johnson and co-workers (1974) and Williamson and Moulis (1994) document 19 species based on voucher specimens. Additionally, we confidently accept the following observations of *H. squirella* (R. Moulis) and *A. carolinensis, Cemophora coccinea, Storeria dekayi, Chelydra serpentina, M. terrapin, Trachemys scripta,* and *K. subrubrum (*Seyle, 1996). The 27 reptiles and amphibians of Blackbeard Island constitute 25% of the coastal fauna.

Sapelo Island is the third largest of the Pleistocene islands and includes approximately 4,415 hectares of upland habitats. The State of Georgia owns the island. It is accessible only by boat, but it is home to approximately 100 residents. The herpetofauna was reviewed by Martof (1963), who reported 36 species of terrestrial amphibians and reptiles. Teal and Teal (1964) provided a popular account of the island including 26 terrestrial amphibians and reptiles, based upon their observations; however, they do not include any species not listed by Martof (1963). The Johnson and co-workers (1974) review included 38 terrestrial amphibians and reptiles from Sapelo Island. Finally, Williamson and Moulis (1994) and Laerm and co-workers (1999) documented additional species bringing the total to 44. These represent 41% of the mainland fauna (Tables 1 and 2). All but three species from Sapelo Island (*Opheodrys aestivus, Seminatrix pygaea,* and *C. serpentina*) are documented by voucher specimens. Amphibian and reptile records from three archaeological sites on Sapelo are discussed below.

Wolf Island consists primarily of extensive marshes bisected by creeks. It has very limited upland areas, approximately 120 hectares. It is of Holocene origin. The herpetofauna of the island has not been well documented. Neill (1948) refers to the presence of *Ophisaurus compressus* occuring along the beach and in tidal wrack. Numerous *C. adamanteus* are on the island.

M. terrapin has been observed on Wolf Island (Harris, 1996). No additional published records or voucher specimens are available. Wolf Island has the lowest percentage of mainland species (3%).

Little St. Simons Island, located to the north of St. Simons, includes 485 hectares of Holocene uplands. The island is not accessible by bridge and has not been developed, except for a small residential/recreational community. It is separated from Sea Island and St. Simons Island to the south by the Hampton River. The only published records of amphibians and reptiles from the island include two historical references documenting the presence of *C. adamanteus* (Anonymous, undated; Leigh, 1883). Additional observations by J. Crawford (1996) and J. Jensen include *Bufo terrestris, H. cinerea, H. squirella, Rana sphenocephala, Gastrophryne carolinensis, A. mississippiensis, O. ventralis, O. compressus, A. carolinensis, E. laticeps, Scincella lateralis, C. sexlineatus,* E. obsoleta, *C. constrictor, Masticophis flagellum,* and *Lampropeltis getula, A. piscivorus,* and *K. subrubrum,* none of which are supported by vouchers. The 20 species represented on Little St. Simons constitute 19% of the mainland fauna.

Sea Island, consisting of 930 hectares of uplands, has been highly impacted by residential and recreational development. It is of Holocene origin and is separated from St. Simons to the west by Village Creek and marshland. It is accessible by bridge. Records of one toad, one lizard, three snakes, and a turtle are based on museum records (Williamson and Moulis, 1994). These constitute 5.61% of the mainland fauna (Tables 1 and 2).

St. Simons Island is the second largest of the sea islands, including approximately 4,980 hectares of uplands. It is of Pleistocene origin. Johnson and co-workers (1974) did not report any terrestrial amphibians and reptiles from the island. Seyle (1985b) reported on the occurrence of *Ambystoma talpoideum.* Additionally, museum voucher specimens documented by Williamson and Moulis (1994) included 10 anurans, one salamander, one lizard, 14 snakes, and two turtles. More recently Campbell and Hammontree (1995) and Campbell (1996) documented established populations of the brown anole, *A. sagrei,* in coastal Camden and Glynn counties, including St. Simons Island. These authors suggest the populations represent recent propagules from Florida nursery vegetation. The St. Simons' fauna represents 27% of the mainland fauna. Additional pre-modern records from eight archaeological sites are documented below.

Jekyll Island is the smallest of the Pleistocene islands with approximately 1780 hectares of uplands. Jekyll, too, has experienced considerable impact through residential and recreational development. It is accessible from the mainland by bridge. Johnson and co-workers (1974), Anderson and co-workers (1976), Kiviat (1982*a,b,c,d,e*), and Taylor Schoettle (1984) provide published records for numerous species. These, coupled with the museum voucher records of Williamson and Moulis (1994), and personal observations now total 31 species: 10 amphibians, the alligator, seven lizards, 11 snakes, and two turtles (Tables 1 ands 2), constituting 29% of the mainland fauna.

Little Cumberland Island is separated from its larger neighbor, Cumberland Island, to the south by Christmas Creek. It is privately owned and has limited residential development. It is of Holocene origin and encompasses approximately 650 hectares. Johnson and co-workers (1974), Hillestad and co-workers (1975), and Mann and Kraemer (1979) documented the first records from Little Cumberland Island. Williamson and Moulis (1994) reviewed museum voucher records. With 32 species including seven frogs and toads, one salamander, the alligator, seven lizards, 13 snakes and three turtles (several of which are unsubstantiated by voucher documentation), Little Cumberland Island boasts the highest species richness among the Holocene Islands, thus constituting 30% of the coastal fauna.

Cumberland Island is the largest of the Pleistocene islands with 6,115 hectares of uplands. It is administered as a National Seashore and Wilderness Area, although portions of the island are privately owned and support light residential development. Access is limited. Johnson and co-workers (1974), Hillestad and co-workers(1975), and Shoop and Ruckdeschel (1986) provide records for the herpetofauna of the island. Shoop and Ruckdeschel (1986) note that several species reported by Johnson and co-workers (1974) and Hillestad and co-workers (1975) are unsubstantiated by voucher specimens. These include: *B. quercicus, H. chrysoscelis, Pseudacris nigrita,* and *O. compressus.* They also note that the attribution of *Pituophis melanoleucus* to Cumberland Island by Hillestad and co-workers (1975) is incorrect. The specimen is a juvenile *E. obsoleta.* Thus, 15 anurans, five salamanders, the alligator, 10 lizards, 17 snakes, and nine turtles are reported from Cumberland Island (Tables 1 and 2). The 57 species constitute the highest proportion (53%) of mainland fauna found on a Georgia barrier island. Additional premodern archaeological records are discussed below.

Georgia sea island herpetofauna in the regional perspective—Some 43 amphibians occur in coastal Georgia, including 25 anurans and 18 caudates. Fewer amphibians, relative to their number on the mainland, occur on the sea islands: 17 anurans and 8 caudates. These comprise 58% of the mainland fauna. Amphibians as a group have been less successful colonizers of the sea islands compared to reptiles which have 64 mainland forms, of which 47 (73%) are represented on the islands.

Anura—All families of anurans which occur on the mainland are represented on the sea islands, including 100% of the bufonid species, 71% of the hylids, 43% of the ranids, and 100% each of the microhylids and pelobatids. The anurans are more successful colonizers of the islands than the caudates: 68% of the mainland anurans occur on islands, compared with only 44% of the caudates.

Bufonidae—Coastal toads are represented by two species: *B. quercicus* and *B. terrestris.* The latter is the more widely distributed on the Sea Islands. It is documented from 12 islands (making it one of the three most widely distributed of the Georgia insular herpetofauna) while the former is reported only from three islands (Table 1). The occurrence of *B. terrestris* on all of the larger Pleistocene islands and six of the smaller Holocene islands suggests high colonization ability, compared to *B. quercicus* which is reported only from three of the larger Pleistocene islands. *Bufo terrestris* was reported from Kiawah (but not Capers) Island in South Carolina by Gibbons and Harrison (1981). However, these authors did not report *B. quercicus* from either of those islands. Erhardt (1976) indicated both species were common on Merritt Island, Florida.

Hylidae—Fourteen treefrogs occur on the coastal mainland, 10 of which are reported from the Georgia sea islands. Both species of *Acris,* five of the six *Hyla,* and three of the six *Pseudacris* that occur on the mainland have been reported from the sea islands (Table 1). Williamson and Moulis (1994) document records of *A. crepitans,* from several southeastern Georgia counties, but the only coastal records are from mainland McIntosh County and St. Simons Island. The latter is the only insular record for a South Carolina-Georgia-Florida barrier island. *A. gryllus* does not appear to be a good colonizer either, as it is present on only two of the larger islands, Cumberland and St. Simons (Gibbons and Coker, 1978; reported this absent from Atlantic coastal islands). Gibbons and Harrison (1981) did not report *A. gryllus* from either Capers or Kiawah islands; however, Erhardt (1976) indicated it to be common on Merritt Island and Neill (1958) remarked that this species has been found within approximately 20 m of the ocean.

Pseudacris crucifer and *P. nigrita,* occur on only three and two Georgia sea islands, respectively, while *P. ocularis* is present on six. All *Pseudacris* records are from larger Pleistocene islands. Gibbons and Harrison (1981) do not record *Pseudacris* from either of the South Carolina islands, although Erhardt (1976) reports *P. nigrita* and *P. ocularis* common on Merritt Island. None of the remaining *Pseudacris* have been reported from other regional barrier islands.

Compared to the other hylid genera, species in the genus *Hyla* appear to be more successful colonizers, particularly *H. cinerea,* and *H. squirella,* as they are documented from 11 and 12 of the islands, respectively, including some of the smaller Holocene islands. *Hyla gratiosa* and *H. femoralis* are documented from four and five of the islands, respectively. *Hyla chrysoscelis* is reported only from Cumberland Island (Hillestad, 1975), but the species is not yet substantiated by vouchers (see Shoop and Ruckdeschel, 1980). Gibbons and Harrison (1981) report *H. cinerea* and *H. squirrela* from Kiawah and Capers islands; Erhardt (1976) reports *H. cinerea, H. femoralis, H. gratiosa,* and *H. squirella* from Merritt Island. Neill (1958) has noted that *H. squirella* occasionally breeds in ponds subject to salt spray in the Florida

Keys and added that *H. cinerea, H. femoralis,* and *H. gratiosa* breed in brackish marshes. Noble and Hassler (1936) also recorded *H. cinerea* and *H. versicolor* breeding in slightly brackish water.

The absence of more hylid species on coastal islands may be related to their dependence on permanent freshwater aquatic habitats (Gibbons and Coker, 1978). This is available generally only on the larger islands. However, compared to other families of amphibians, hylids are successful colonizers (71% of the mainland forms are on the islands).

Ranidae—Seven ranids are known from coastal Georgia, but only three are reported from barrier islands. *Rana sphenocephala* is the most common and is reported from 10 (including four smaller Holocene) Georgia sea islands, *R. grylio* from four, and *R. catesbeiana* from two (Table 1). Neither of the latter two species are known from smaller Holocene Georgia islands. Gibbons and Coker (1981) documented only *R. sphenocephala* for the South Carolina sea islands, while Erhardt (1976) indicated that *R. sphenocephala* and *R. grylio* were common on Merritt island. Both these species have been reported as capable of resisting a certain amount of salt water (Viosca, 1923). The low species richness of *Rana* on the sea islands, compared to the mainland, has been attributed to the dependence of many species on standing water for breeding and metamorphosis (Gibbons and Coker, 1978).

Microhylidae and Pelobatidae—Gastrophryne carolinensis and *S. holbrookii* have been recorded from nine and eight of the Georgia sea islands, respectively, including several smaller Holocene islands (Table 1). *Gastrophryne* was recorded on both Kiawah and Capers islands as well as Merritt Island, but *Scaphiopus* was reported only from Kiawah Island (Erhardt, 1976; Gibbons and Harrison, 1981). Both species appear to be good colonizers. *Gastrophryne carolinensis* is known to breed in slightly brackish water (Viosca, 1923; Noble and Hassler, 1936; Neill, 1958).

Caudata—Some 18 species of salamanders occur in coastal Georgia, but only eight have been reported from the sea islands (Table 1). All families documented from the mainland are represented on the islands, including 25% (1 of 4) ambystomatids, 100% (1 of 1) amphiumids, 50% (4 of 8) plethodontids, 50% (1 of 2) salamandrids, and 33% (1 of 3) sirenids.

As pointed out by Gibbons and Coker (1978), salamanders have the lowest colonization rate of all Georgia amphibians and reptiles. "The limited distribution and occurrence of salamanders on coastal islands is readily explained by their intolerance of salt water and xeric conditions. Of the numerous species of reptiles and amphibians which Neill (1958) noted as having been reported in association with brackish or salt water, the only salamanders of those occurring along the Atlantic Coast were in the genus *Siren.* The fact that isolated species have been reported from the islands indicates that suitable conditions do occur in some instances for the establishment of and continued maintenance of salamander populations" (Gibbons and Coker 1978:229).

Information available to Gibbons and Coker (1978) at the time may have underestimated the occurrence of caudates on islands. They reported only 6 (28%) of 21 mainland species occuring on islands from Virginia to Georgia. We document eight (44%) of the 18 Georgia mainland species on the sea islands. Several of the larger islands (Cumberland and St. Catherines islands with four species and Ossabaw Island with five species) exhibit moderate caudate richness, but, in general, caudates are rare on the islands. Gibbons and Harrison (1981) document only one species (*Plethodon glutinosus* [= *grobmani*] from Kiawah Island. Erhardt (1976) does not report any caudates from Merritt Island.

Except for *Notopthalamus viridescens* (recorded from Little Cumberland Island), all documented occurrences of caudates on the Sea Islands are on the larger Pleistocene islands. The central newt is the most widely distributed of the caudates, occurring on the most (five) islands. *Eurycea quadridigitata* and *Amphiuma means* are documented from three islands. The remaining five species are documented from only one island (*Desmognathus auriculatus, E. cirrigera,* and *S. lacertina*) or two islands (*A. talpoideum* and *P. grobmani*).

Reptiles—Lacertilia—Compared to other amphibian and reptile groups, lizards have been very successful colonizers. The 13 species documented from Georgia sea islands comprise 84.62% of the mainland fauna, including 50% (2 of 4) of the anguids, and 100% of the polychrids (2 of 2), scincids (5 of 5), phrynosomatids (1 of 1), and teiids (1 of 1; Table 1). The successful colonization of islands by lizards may be due to their small body size, propensity for association with rafting materials, tolerance for saline and xeric conditions, and the fact that they are largely insectivorous (Gibbons and Coker, 1978), permitting them foraging opportunities in all but the most barren habitats. This is reflected in the fact that all but four species (*O. attenuatus, O. mimicus, E. egregius,* and *A. sagrei*) are documented on three or more islands including several of the smaller Holocene islands.

Anguidae and *Geclionidae*—Glass lizards (*O. mimicus,* and *O. attenuatus*) include the only mainland species that have not been documented from Georgia barrier islands. However, *O. ventralis* is one of the most common insular species, occuring on 10 of the islands. The island glass lizard is reported from five Georgia islands. Gibbons and Harrison (1981) report *O. ventralis* from both Kiawah and Capers islands. Similarly, Erhardt (1976) reports *O. ventralis* as an occasional inhabitant of the flatwoods of Merritt Island, but comments *O. attenuatus* to be common. In so far as we can determine, this is the sole record of the latter from a barrier island. The introduced Mediterranean gecko (*Hemidactylus turcicus*) is present in the Savannah and Brunswick areas, but there are no records from the islands.

Polychridae—Anolis carolinensis, a common mainland species, is documented from 11 of the islands. In fact, it is the most common lizard on the Georgia sea islands. Gibbons and Harrison (1981) and Erhardt (1976) indicate *A. carolinensis* occurs commonly, but neither record *S. undulatus* in their respective studies. *Anolis sagrei* has only recently expanded its range into Georgia (see Campbell and Hammontree, 1995; and Campbell, 1996 for details and review of the recent range expansions). The apparent ease by which it is transported and becomes established as a propagule from Florida nursery vegetation suggests it may become more widely established from additional introductions and expansion of founder populations, particularly on islands with residential and commercial development.

Scincidae and *Phrynosomatidae*—All species of mainland skinks are represented on the islands. With the exception of *E. egregius* which is documented from only one island (Cumberland; Erhardt, 1976) and *E. fasciatus,* reported from four islands, the remainder (*E. inexpectatus, E. laticeps,* and *S. lateralis*) are known from eight or ten of the larger Pleistocene and smaller Holocene islands (see Table 1). Gibbons and Harrison (1981) report the latter three species from both Kiawah and Capers islands. Erhardt (1976) noted *E. egregius* on Merritt Island as well as *E. inexpectatus* and *S. lateralis. Sceloporus undulatus,* which is also common and widely distributed on the mainland, is documented from only three islands (see Table 1).

Teiidae—Cnemidophorus sexlineatus is documented from nine Georgia islands as well as those of South Carolina and Florida (see Table 1).

Serpentes—Twenty-three (71%) of the 34 mainland snake species are recorded from Georgia Barrier islands. Insular species include 68% (19 of 28) of the colubrid, 100% (1 of 1) of elapid, and 60% (3 of 5) of the viperid mainland species. Of the 24, nine occur on more than half of the sea islands. Six species (*C. constrictor, E. obsoleta, L. getula, T. sauritus, A. piscivorus,* and *C. adamanteus*) are documented from 10 or more islands, including four to six of the smaller Holocene islands (see Table 1). Several other species (*C. coccinea, E. guttata, Nerodia fasciatus, O. aestivus,* and *T. sirtalis*) appear to be moderate to good colonizers as they are known from seven to eight islands, including, in all cases, at least two or three smaller Holocene islands. On the other hand, some species appear to be poor colonizers. Eleven species are known only from one to four islands. All but two of these (*Rhadinaea flavilata* and *S. dekayi)* are restricted to larger Pleistocene islands. Despite the success of some species of snakes in insular colonization, 10 mainland species are not documented from islands (Table 1). Sandifer and co-workers (1980) suggest that many species of aquatic and small, cryptic snakes may be poor colonizers due to osmoregulatory problems associated with crossing extensive areas of salt or brackish waters. Also, some of these snakes like *S. occipitomaculata, T. coronata, Diadophis punctatus,* and

M. fulvius are semi-fossorial and associated with dense litter and coarse woody debris. Dependence upon such habitat features may limit colonization opportunities. Alternatively, these species may be present on many of these islands, but because of their fossorial nature, have not been documented as of yet.

Colubridae—The colubrids are the most diverse family of reptiles regionally representing 19 genera and 28 species. As a group they exhibit mixed success as colonizers. Four of the top six insular snake colonizers are colubrids. Six of the top 13 amphibian and reptile colonizers (as judged by being present on 10 or more islands) are colubrids. However, there are some notable exceptions. Nine of the 12 species of snakes not documented from islands are colubrids. Gibbons and Harrison (1981) list 11 colubrids occurring on Capers and Kiawah islands, only three of which occur on both islands: *C. constrictor, E. obsoleta,* and *N. fasciata.* They are among the most successful colonizers of Georgia islands as well. Only one species (*T. coronata*) is documented on either Kiawah or Capers islands that does not occur on one or more Georgia islands. In contrast, Erhardt (1976) lists 18 colubrids from Merritt Island, five more than the most colubrid-rich island in Georgia. Two species are documented from Merritt Island which are not known from Georgia islands: *Regina rigida* and *P. melanoleucus.*

Elapidae—Micrurus fulvius is known only from Ossabaw Island. It has not been reported from Florida or South Carolina islands, although Obrecht (1946) noted it from the mainland in Myrtle Beach, South Carolina. This species may be present on some of the islands but because of its fossorial and secretive nature, may not have been discovered yet.

Viperidae—Three of the five mainland viperids are reported from the Georgia sea islands. *Agkistrodon piscivorus* and *C. adamanteus* are among the most successful reptile and amphibian colonizers and are present on 10 and 13 of the Georgia islands, respectively. *Crotalus horridus* is documented from four Georgia islands. We know of no records of *A. contortrix* on Georgia sea islands. Although Gibbons and Harrison (1981) report it from Kiawah Island, it is not known from North Carolina Islands or Merritt Island to the south. *Sistrurus miliarius* is also not documented from Georgia islands, although Erhardt (1976) reports it common in a variety of habitats on Merritt Island.

Crocodylia—Alligator mississippiensis is widely distributed on Georgia barrier islands, having been documented from all but three of the islands. The tolerance of the alligator to brackish or salt water is well known (Neill, 1958; Gibbons and Coker, 1978).

Testudinata—Eleven of the 16 regional terrestrial turtles are documented from the sea islands, including 100% (1 of 1) of the chelydrids, 75% (6 of 8) of the emydids, 50% of the kinosternids (2 of 4), the gopher tortoise, and 50% (1 of 2) of the tryonichids (Table 1). However, five of the species of turtles reported from Georgia sea islands are restricted to a single island. Only *K. subrubrum* and *M. terrapin* occur on more than half of the islands; the former occuring on ten and the latter on 12. Both Gibbons and Coker (1978) and Sandifer and co-workers (1980) comment on the comparative low colonization of a number of otherwise widely distributed turtle species compared to other reptiles. They suggest this may be due to the absence of fresh water during severe droughts or periods of saltwater flooding. Also, Sandifer and co-workers (1980) point out that raccoons, *Procyon lotor,* are known to be a significant predator to marine turtle eggs and may prey heavily on the eggs of terrestrial turtles. It is not clear, however, why several widely distributed mainland species such as *Clemmys guttata, Sternotherus odoratus,* and *Terrapene carolina* are not well represented on islands.

K. baurii is also not well represented on the islands but this may be due to the difficulty of distinguishing them from *K. subrubrum.*

Chelydridae—*Chelydra serpentina* is known from six Georgia islands, suggesting it to be a moderately successful colonizer. No chelydrids were reported from Kiawah and Capers islands.

Emydidae—*Deirochelys reticularia* is reported from 6 Georgia islands. *Deirochelys* is reported as common on Merritt Island (Erhardt, 1976). *Malaclemys terrapin* is a coastal specialist and has been documented from 12 of the islands. *Trachemys scripta* is reported from five islands, but the other emydids are restricted to a single island each (Table 1). *Pseudemys floridana* has yet to be documented from islands. The very common mainland *T. carolina* is rare on islands. In Georgia it is reported only from Sapelo Island. It is documented on Kiawah and Merritt islands but not on any of the North Carolina islands (Gibbons and Coker, 1978; Erhardt, 1976).

Kinosternidae—*Kinosternon subrubrum* is present on 10 of the Georgia islands as well as both South Carolina and Florida islands. *Kinosternon baurii* is rare on Georgia islands. It is documented only from Cumberland. However, Erhardt (1976) notes it to be common on Merritt Island. Pope (1939) suggested it thrived in coastal brackish water. Neither *S. minor* or *S. odoratus* have been reported from islands. *Sternotherus minor* is primarily a steam species and is probably not present due to lack of available habitat.

Testudinidae—*Gopherus polyphemus* is common in scrub and flatwoods habitats on Merritt Island (Erhardt, 1976) but apparently has not been a successful colonizer of the Georgia islands. Its presence on some of the islands is reportedly due to introductions (Cumberland: Johnson et al., 1974; St. Catherines: Winn, 1996).

Trionychidae—*Apalone ferox* is reported only from Cumberland and Merritt islands. These highly aquatic turtles commonly inhabit fresh and mildly brackish habitats. There are no reports of *A. spinifera* from islands. However, Neill (1958) noted this species enters brackish water frequently.

Prehistoric and historic occurrences of amphibians and reptiles on the Georgia Sea Islands—Faunal debris is often a significant component of materials excavated at archaeological sites. Because of the long temporal span over which faunal components may be deposited at archaeological sites, such records have particular utility and application in understanding the historical occurrence and distribution of individual species and community structure (Reitz et al., 1996). The southeastern United States and Georgia, in particular, have a rich archaeological heritage. Within Georgia approximately 15,000 archaeological sites are known. The vast majority of these have not been excavated. Thirty-seven sites in Georgia have been the focus of zooarchaeological analysis (Data bases of the University of Georgia Museum of Natural History). We summarize here amphibian and reptile faunal remains recovered from the 17 excavated and analyzed archaeological sites on three Georgia sea islands. These include one site on Cumberland Island, three on Sapelo, eight on St. Simons Island, and five on St. Catherines. The temporal distribution ranges from Archaic 2240 BC to 18th century Colonial Period. Faunal records identified to species from these sites are discussed below. These records were not included in calculations of species richness or in area-species relationships. Additional faunal elements not identified to species or genus are not included. Copies of all faunal reports and records on file, University of Georgia Museum of Natural History.

Cumberland Island—Milanich (1980) reported *Deirochelys reticularia, M. terrapin, T. carolina, A. ferox,* and *G. polyphemus* from a Deptford single house and other Woodland sites on Cumberland Island dating from 1100 BC to 1000 AD. In addition, several terrestrial herps not identified to species included *Sternotherus* spp. and *Pseudemys* spp.

Deirochelys reticularia, M. terrapin, and *A. ferox* are currently known from Cumberland Island. *Gopherus polyphemus* also occurs on the island, but this population is reported to have resulted from recent introductions (Johnson et al., 1974; Hillestad et al., 1975). *Terrapene carolina* and *Sternotherus* spp. are not presently known from Cumberland Island. There are no modern *Sternotherus* records for any barrier island from Florida to North Carolina (Gibbons and Coker, 1978).

Sapelo Island—Three Sapelo Island sites have been the subject of zooarchaeological analyses: Kenan Field, Bourbon Field, and North of the Shell

Ring Drain (Reitz, 1982). They are roughly of comparable age: Mississippian, primarily Savannah (1150–1300 AD) and Irene. There is controversy regarding the date of Irene Phase sites. Traditionally, Irene has been considered to post-date DeSoto's arrival in 1540–1680 but more recently has been expanded to include late Mississippian occupation (AD 1300–1540).

Malaclemys terrapin was then, as now, a common faunal componant on Sapelo Island as it is present at all three sites. *Kinosternon subrubrum* and *D. reticularia,* still common on Sapelo Island, are documented from two of the sites. *Anolis carolinensis, C. constrictor, A. piscivorus, A. mississippiensis, T. carolina, K. subrubrum,* and *A. ferox,* are documented from single sites. All but *Apalone* are documented modern components of the fauna.

St. Catherines Island—Analysis of five excavations from St. Catherine's are available. Three of these are derived from transect studies and include an Archaic (St. Simons Period) dating from 2200 to 1100 B.C., Woodland (actually a series of smaller sites, including Refuge, Deptford, and Wilmington periods) dating between 1100 BC and 500 A.D., and Mississippian (Savannah) dating from 1150 A.D. to 1300 A.D. (Reitz, 1989). Two additional Spanish settlement sites are described by Reitz and Duncan (1993).

Malaclemys terrapin, A. mississippiensis, and *Kinosternon* spp. were the most common species reported across sites, and are modern faunal components. *Chelydra serpentina, T. carolina, G. polyphemus,* and *A. ferox* are present in the archaeological record but have not been documented from St. Catherines in recent times (although *Gopherus* has recently been introduced).

St. Simons Island—Martinez (1975) reported on a series of six Middle to Late Mississippian (Wilmington and Deptford) shell midden sites from Cannon's point on St. Simons Island dating from 500 BC to 1000 AD. Additional Cannon's Point Shell Ring sites were reported on by Marrinan (1975). These include a series of Late Archaic sites (2240–1665 BC). The Couper Field Irene site described by Wallace (1975) contained no amphibian or reptile remains. In addition to these, several historic excavations on St Simons yielded additional evidence for the occurrence of species in early settlement times: Otto (1975) and McFarlane (1975) at two Cannons Point sites dating from the turn to middle of the 18th century; Moore (1981) from Butler Point, also early 18th century; and two excavations at Fort Frederica dating from the first half of the 17th century (Honerkamp, 1982; Reitz and Honerkamp, 1983).

Malaclemys terrapin, was the most common species of herpetofauna present, followed by *A. mississippiensis, D. reticularia,* and *Kinosternon* spp. Several species were recovered from at least two sites: *C. constrictor, T. scripta, G. polyphemus* and *A. ferox.* Single site records were reported for *R. sphenocephala, Siren* spp., *A. carolinensis, D. corais, P. melanoleucus, C. serpentina, Pseudemys* cf. *floridana, T. carolina,* and *Sternotherus* spp.

Pituophis melanoleucus, the possible *P.* cf. *floridana,* and *Sternotherus* spp. have not been reported as modern components on any of the Georgia sea islands. The *D. corais* record from St. Simons is the only pre-historic record of the species on a barrier island. *Siren* spp., *A. carolinensis, Nerodia, C. serpentina, D. reticularia, T. carolina, T. scripta, Sternotherus* spp., and *A. ferox,* are documented on one or more of the other barrier islands. They have not been reported from St. Simons in modern times, although they would be expected components of the fauna.

Examination of the zooarchaeological records for these islands indicates numerous historic records of species expected to occur on many if not most of the barrier islands but for which there is no contemporary documentation. These records are biased toward species that made up a significant part of the subsistence pattern of inhabitants of the region at time of deposition. There also is no assurance that the presence of species in the Native American and/or European colonial archaeological sites on a particular island is *prima facie* evidence that such species actually occurred on that island at the time of deposition. For example, it cannot be determined if a particular species was obtained elsewhere and brought to the island. In fact, the archaeological records of some species can only be explained by human transport. It is well known that *G. polyphemus* made up a significant portion of the diet of Europeans in Spanish Florida: 32% of the wild terrestrial species exploited at St. Augustine (Reitz and Scarry, 1985). *Gopherus* was widely transported and has been documented from Spanish settlements beyond their range, such as at Santa Elena, South Carolina (Reitz, 1984). Two of the three insular zooarchaeological records of this species are from European settlements; however, the Cumberland Island record is Woodland. Similar concerns might be expressed for other species, particularly the turtles which are the predominant species at these sites. Nonetheless, the significant numbers of zooarchaeological records at these sites suggest either a number of species had more extensive ranges in the past or, alternatively, the present distribution of amphibians and reptiles on these islands is not fully documented.

Influence of size, age, study, and environmental impacts in structuring the richness of insular herptofaunal communities—As a group, the islands of Pleistocene origin have a higher species richness of amphibians and reptiles compared to younger Holocene islands (Table 3). A total of 68 species are documented from the six islands of Pleistocene origin compared to the 37 species known from Holocene islands. Except for the alligator, each taxonomic group has a greater number of species represented on the Pleistocene islands compared to Holocene islands. The Pleistocene islands as a group constitute 64% of the mainland fauna, and the percentage composition of the herpetofauna by taxonomic groups on these islands is not significantly different from that of the mainland (Table 3). The Holocene islands as a group constitute only 35% of the mainland fauna, but the percentage com-

TABLE 3. Percentage composition of Georgia Sea Islands and mainland herpetofauna by taxonomic group.

Group	Mainl	Tyb	L Ty	Wass	Oss	St C	Blbrd	Sap	Wolf	Sea	L SS	St S	Jekyll	L Cu	Cu
Anura	23.36	31.25	12.50	16.00	25.00	24.32	18.52	26.67	0.00	16.67	26.32	37.93	32.26	21.88	26.32
Caudata	16.82	0.00	0.00	0.00	12.50	10.81	0.00	4.44	0.00	0.00	0.00	3.45	0.00	3.12	8.77
Crocodilia	0.93	6.25	12.50	4.00	2.50	2.70	3.70	2.22	0.00	0.00	5.26	0.00	3.23	3.12	1.75
Lacertilia	12.15	18.75	25.00	16.00	17.50	16.22	22.22	20.00	50.00	16.67	31.58	3.45	22.58	21.88	17.54
Serpentes	31.78	31.25	37.50	44.00	30.00	32.43	40.74	35.56	0.00	50.00	26.32	48.27	35.48	40.63	29.82
Testudinat	14.95	12.50	12.50	20.00	12.50	13.51	14.81	11.11	50.00	16.67	10.53	6.90	6.45	9.37	15.79
Total	99.99	100.00	100.00	100.00	100.00	99.99	99.99	100.00	100.00	100.01	100.01	100.00	100.00	100.00	99.99

position of the herpetofauna by taxonomic groups on these islands is not significantly different from the mainland. Absolute values for salamanders would suggest they are under-represented on the islands and that lizards are over-represented; however, they are not significantly different from their relative proportion on the mainland. The similarity of percent composition of both the Pleistocene islands and Holocene islands to the mainland indicates colonization of the Georgia barrier islands has been in approximate (statistical) proportion to their abundance on the mainland.

Classic island biogeography models predict relationships between species richness and island size and distance to mainland source of colonizers (MacArthur and Wilson, 1967). Direct comparisons of species richness and community composition of the amphibians and reptiles of the Georgia sea islands and the mainland must be made cautiously. While considerable data on insular species richness are now available for the Georgia islands as summarized here, we do not know to what extent these data may be biased. At the very least, existing knowledge of species richness and community composition would be expected to be biased by unequal sampling efforts. Some islands have had significant attention, others have had little. It is also likely that various land management practices (both present and past) as well as the degree of agricultural, residential, and/or recreational development would impact species richness. However, additional abiotic features, such as island size and distance to the mainland (and other islands) as predicted by island biogeography models as well as different ages of the island (Holocene versus Pleistocene) would also be expected to account for differences seen between separate islands and islands as a group compared to the mainland. Furthermore, biotic features relating to area-species richness phenomena, such as availability and extent of various habitat types, would also be expected to account not only for species richness but also community composition as well.

Values for island areas are shown in Table 1. Qualitative assessments of the degree of herpetological study and environmental impact assigned to the respective islands are shown in Table 4.

Area-species relationships of the sea islands based on un-transformed data provided in Table 2 show highly significant values ($p< 0.05$) and goodness of fit for all iterations (Table 5a), except lizards. As a group, lizards exhibit the highest percentage of colonization of available mainland species compared to other groups (only two species are not represented on the islands). All but three species of lizards are documented from four or more islands including several of the smaller islands. Their high richness on most of the islands would account for the non-significance in the regression model. Urodeles as a group show the lowest percentage of colonization of available mainland species, yet they exhibit a highly significant species-area relationship. Thus, island size is highly significant in predicting species richness.

Regression analysis of species richness against distance from mainland

TABLE 4. Percentage composition of Georgia Sea Island herpetofauna by taxonomic group based on island age (Holocene or Pleistocene).

Group	Number of species on mainland	Percentage of mainland species by group	Number of species on Pleistocene islands	Percentage of Pleistocene island species by group	Number of species on Holocene islands	Percent of Holocene island species by group
Anura	25	23.36	17	25.00	7	18.92
Caudata	18	16.82	8	11.76	1	2.70
Crocodylia	1	0.93	1	1.47	1	2.70
Lacertilia	13	12.15	11	16.18	8	21.62
Serpentes	34	31.78	21	30.88	14	37.84
Testudinata	16	14.95	10	14.71	6	16.22
Total	107	99.99	68	100.00	37	100.00

TABLE 5. Qualitative assessments of the degree of herpetological study and environmental impact assigned to respective Georgia Sea Islands by three independent observers. Ranking between 1 and 5; 1 lowest, 5 highest. See text for details.

	Study		Impact	
	Mean	Range	Mean	Range
Tybee	2.33	2–3	4.67	4–5
Little Tybee	1.33	1–2	1.33	1–2
Wassaw	2.67	2–3	1.33	1–2
Ossabaw	3.00		3.33	3–4
St Catherines	3.67	3–4	3.00	
Blackbeard	2.33	2–3	2.00	
Sapelo	3.67	3–4	3.67	3–4
Wolf	1.33	1–2	1.00	
Little St Simons	2.33	2–3	2.33	2–3
St Simons	2.33	2–3	2.00	
Sea	2.00		4.00	3–5
Jekyll	2.33	2–3	3.67	3–4
Little Cumberland	4.00		2.00	
Cumberland	4.67	4–5	2.67	2–3

and distance from nearest neighbor island indicated no significant relationships. While distance to mainland is a predictor of island species richness in most insular biogeography models (MacArthur and Wilson, 1967), we suggest the most parsimonious interpretation of the lack of significance in our regression model is that distances between the various Georgia sea islands and mainland are too small to have an impact on species richness.

We hypothesized that eliminating smaller Holocene islands from our analysis might improve predictability of the relationship of richness and distance to the mainland. Only two groups showed significant linear relationships. The anurans and snakes both showed a significant negative relationship between distance from mainland and richness ($p = 0.0055$, R-square $= 0.6904$) and ($p = 0.0030$, R-square $= 0.677$), respectively.

Simple linear regression of "amount of study" against richness show highly significant values ($p < 0.05$) and goodness of fit for all iterations (Table 5b). However, similar analysis for "impact" failed to yield significant values for any groups. Disturbance level as we defined it is not a significant predictor of species richness on the islands.

Multiple (stepwise) linear regression of species richness to the independent variables (size, degree of study, impact) improved predictability of species richness compared to the simple linear models (Table 5c). Total species richness (all groups combined) was best predicted by size and study. Similarly, amphibians (as a group), anurans, caudata, snakes, and turtles were also best predicted by size and study. Only lizard species richness was not improved by any variable beyond study. These data suggest that island size and amount of study are the most important factors in predicting perceived insular herpetofaunal richness.

TABLE 6. Simple linear regessions of species richness of Georgia barrier islands based on island upland area derived from non-transformed data from Table 2.

Model	Regression	p	R^2
All species	$y = 13.0932 + 0.0062x$	0.0004	0.6592
Amphibia	$y = 2.0836 + 0.0027x$	0.0001	0.8048
Reptilia	$y = 11.0947 + 0.0036x$	0.0029	0.5374
Anura	$y = 2.4899 + 0.0019x$	0.0001	0.7427
Caudata	$y = -0.4063 + 0.0008x$	0.0006	0.6360
Crocodylia			
Lacertilia	$y = 3.3648 + 0.0007x$	0.0713	0.2459
Serpentes	$y = 5.2816 + 0.0020x$	0.0010	0.6085
Testudinata	$y = 1.6031 + 0.0008x$	0.0049	0.4967

SUMMARY—The data presented here represent the most comprehensive summary of known records of amphibians and reptiles of Georgia sea islands. New records continue to be documented, even from the well-studied islands. In particular, the records from archaeological sites indicate a number of species have (had) more extensive distributions than can be accounted for on the basis of presently known distributional records. Furthermore, other than anecdotal comments, little information is available regarding community composition of amphibians and reptiles in different habitats on even the most well-studied of these islands (see Laerm et al., 1999). However, the high significance values associated with our regression analyses suggest our present knowledge of species richness on the islands may be fairly accurate.

Coastal islands are under considerable stress from residential, commercial, and recreational development. The impact of these activities on amphibian and reptile communities on barrier islands is uncertain. Gibbons and Harrison (1981) suggested that resort community development has had a negative impact on a number of habitat-sensitive species on Kiawah Island, South Carolina. We did not observe compelling statistical evidence from our analysis that "impact", as we defined it, has significance in structuring herpetofaunal richness. Dodd and Franz (1994) found that in the Bahama Is-

TABLE 7. Simple linear regressions of species richness of Georgia barrier islands based on amount of herpetological study. See text for details.

Model	Regression	p	R^2
All species	$y = -11.3370 + 14.0489x$	0.0001	0.7974
Amphibia	$y = -5.8101 + 5.0892x$	0.0003	0.6843
Reptilia	$y = -5.4256 + 9.0012x$	0.0001	0.8006
Anura	$y = -3.2101 + 3.6573x$	0.0006	0.6394
Caudata	$y = -2.6000 + 1.4319x$	0.0035	0.5233
Crocodylia			
Lacertilia	$y = -1.7593 + 2.4909x$	0.0004	0.6557
Serpentes	$y = -2.1125 + 4.3321x$	0.0002	0.6899
Testudinata	$y = -1.9011 + 1.9377x$	0.0002	0.6966

TABLE 8. Multiple linear regressions of species richness of Georgia barrier islands based on size (X1) and amount of study (X2). See text for details.

Model	Regression	*p*	R^2
All species	$y = -7.4002 + 0.0032(X1) + 9.9624(X2)$	0.0001	0.9098
Amphibia	$y = -3.5417 + 0.0019(X1) + 2.7346(X2)$	0.0001	0.9283
Reptilia	$y = -3.6675 + 0.0014(X1) + 7.1763(X2)$	0.0001	0.8554
Anura	$y = -1.6040 + 0.0013(X1) + 1.9902(X2)$	0.0001	0.8607
Caudata	$y = -2.6739 + 0.0004(X1) + 0.9097(X2)$	0.0010	0.7891
Crocodylia			
Lacertilia	$y = -1.7593 + 2.4909(X1)$	0.0004	0.6557
Serpentes	$y = -0.7761 + 0.0011(X1) + 2.9448(X2)$	0.0001	0.8077
Testudinata	$y = -1.4765 + 0.0003(X1) + 1.4971(X2)$	0.0004	0.7566

lands, the herpetofauna is influenced by island size and anthropogenic factors, but not distance to the nearest large island. They suggest that human related impacts through the introduction of exotic pets (house cats) may alter, at least, populations of certain lizards.

In general, the barrier islands along coastal Georgia with the highest residential, commercial, and recreational development exhibit the lowest absolute richness values (Tybee, Sea, Little St. Simons, St. Simons, and Jekyll). However, with the exception of St. Simons (the second largest at 4,980 hectares), these are among the smallest islands. As a result, it is difficult to separate the influence of species-area relationships and the impact of development on richness values. Even the smaller of the islands with limited contemporary environmental impacts, such as Wassaw, Blackbeard, and Little Cumberland islands, have absolute richness values roughly equivalent to or higher than "impacted" islands of much greater area (such as St. Simons and Jekyll). Furthermore, it is probably impossible to determine the impact that 18th, 19th and early 20th century land management practices (cotton, rice, indigo, other agriculture, lumber, etc.) have had on the islands' present herpetofauna. We would hesitate to suggest environmental impacts would not affect species richness. However, our analyses indicate that other variables (island size and how well they have been studied) are most highly correlated with species richness of these islands as it is currently known.

Attention to the documentation of faunal records is really the first step in addressing issues relating to theoretical aspects of island biogeography as in the case here of amphibians and reptiles on the Georgia sea islands. Inferences regarding conservation issues must also be based upon accurate information. Too often basic descriptive data are inadequate to address the distinction between biological versus anthropogenic factors in controlling such phenomena as biological diversity.

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PREY SELECTION BY A MATERNITY COLONY OF BIG BROWN BATS (*EPTESICUS FUSCUS*) IN THE SOUTHEASTERN UNITED STATES

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Abstract: We examined foraging selectivity of big brown bats (*Eptesicus fuscus*) in a maternity colony located in Clarke County, Georgia. We tested to see if diet differed among four stages of reproduction: pre-parturition, parturition, early lactation, and late lactation. We determined available prey using insect light traps and the diet of the colony by examining fecal pellets. The remains of insects from four of the nine insect orders captured were encountered during fecal analysis: Coleoptera, Lepidoptera, Hymenoptera, and Diptera. The relative availability of three insect orders differed among the four stages of reproduction. The proportion of Coleoptera consumed also differed among the four stages of reproduction. Despite differences in the relative abundance of the three insect orders and the proportion of one insect order consumed during the four stages of reproduction, general foraging patterns of the bats in the colony remained unchanged from pre-parturition to late lactation; the bats consumed more coleopterans and fewer lepidopterans, dipterans, and hymenopterans than expected based on the relative abundance of these orders throughout all stages of reproduction. Thus, the diet of bats may be affected by the differing energetic demands of each reproductive stage. These differences, while statistically significant, may not reflect general foraging preferences.

There is a paucity of information concerning the importance of food as a factor limiting bat populations. Lack of this information limits the ability of biologists to predict the effects of changes in insect communities on bat populations (Fenton, 1997). Big brown bats are one of the most studied bats in North America and the diet of this species has been documented in many regions of the United States (Hamilton, 1933; Phillips, 1966; Whitaker, 1972, 1995). Nevertheless, few studies of its diet have been conducted in the Southeast (Carter et al., 1998) and few researchers have investigated how diet differs throughout the year (Whitaker, 1995).

Temporal shifts in the composition of the diet of bats may be most pronounced surrounding the period of reproduction because pregnant mammals have different nutritional requirements than reproductively inactive mammals (Gittleman and Thompson, 1988; Keeler and Studier, 1992; Kurta et al., 1988). However, little is known concerning the effects of increased energetic demands caused by reproduction on the diet of big brown bats. Our objectives were to determine: (1) the composition of the diet of a maternity colony of big brown bats in the southeastern United States during four stages of reproduction (pre-parturition, parturition, early lactation, and late lactation); (2) if bats in the colony were selectively feeding on available insect prey; and (3) if foraging selectivity differed among four stages of reproduction.

METHODS—This study was conducted from 23 May to 24 June, 1997 in the Piedmont physiographic province of Georgia. The maternity roost was located in the attic of an apartment building in Athens, Clarke County (33°53′N, 83°23′W, Elev. 250 m). Four habitat types dominated the surrounding landscape including bottomland hardwood forests, upland hardwood forests, pine forests, and agricultural areas.

We divided the study period into four segments that reflected the differing energy demands of the maternity colony during different stages of the reproductive cycle. The stages of reproduction were determined by examining the reproductive condition of captured individuals (Racey, 1988) and observations made at the roost. Pre-parturition was from 23 May to 1 June. Parturition was from 2 to 9 June. Early and late lactation were from 10 to 16 and 17 to 24 June, respectively.

Bats were captured using a harp trap (Tuttle, 1974) placed in front of the attic egress. Species, sex, age, mass, and forearm length were recorded for each bat captured. Adults were distinguished from juveniles by the degree of epiphyseal-diaphyseal ossification (Anthony, 1988). Seven adult females were equipped with 0.46-g transmitters (150–151 MHz) from Holohil Systems Limited (Ontario, Canada). The transmitters were attached between the shoulder blades using Skin-bond® brand surgical glue. Transmitter load was below 5% of body mass (Aldridge and Brigham, 1988).

Telemetry stations were established throughout the study area and the Universal Transverse Mercator (UTM) coordinates of each station was obtained using a Trimble Pathfinder Global Positioning System (GPS). Foraging locations were determined by simultaneously taking bearings on foraging bats from two locations using 3-element folding Yagi antennas and R2000 Advanced Telemetry System receivers (Isanti, Minnesota). The UTM coordinates of the telemetry stations and the azimuths of each bearing were entered into program LOCATE to obtain the UTM coordinates of the foraging locations using triangulation (Kie et al., 1996). Foraging locations were plotted on a digital orthograph of the study area using ArcView (Environmental Systems Research Institute, Inc., Redlands, CA). Habitat use was estimated for each reproductive stage using the spatial distribution of foraging points across the landscape (L. R. Jablonowski *unpublished data*).

Aluminum pans were placed under the cluster of bats in the roost. All fecal pellets were removed from the pans at the end of each reproductive period. Thirty fecal pellets randomly selected from each reproductive period were analyzed. To avoid potential bias, an identification number was randomly assigned to each fecal sample so that collection times were unknown during examination. Each sample contained three fecal pellets, which were placed in petri dishes in a 70% ethanol solution and dissected using probes and forceps. Using a dissecting microscope, we identified insect remains in the samples to the ordinal level. A visual estimation of the percent volume of each insect order was recorded for each sample. We estimated the percent volume of lepidopterans as suggested by Whitaker (1988).

Twelve-volt, black-light insect traps were used to collect insect samples from each of the habitat types during each stage of reproduction. Insect traps were suspended 1.5 m above the ground in each habitat type and samples were collected for a minimum of three nights during each reproductive period. Insects were collected from traps daily and frozen. Later, insects were sorted and identified to the ordinal level. We recorded the ocular estimate of the relative volume of the sample composed by each insect order for each habitat type (Whitaker, 1988).

The proportions of insects in fecal pellets have been compared to the proportions of insects captured from areas used by foraging bats (Black, 1974; Brack and LaVal, 1985; Brigham, 1990; Lacki et al., 1995). However, these researchers did not consider the relative amount of time bats spent in each community type. More accurate estimates of the composition of insect communities encountered by bats while foraging can be calculated using the product of the relative amount of time bats spent in each habitat type and the proportion of each insect order in each habitat (Kunz, 1988). We considered both the relative amount of time bats spent foraging in each of the available habitat types and the relative abundance of each insect order in each habitat type when determining availability of insect prey. We calculated the relative amount of time bats spent in each habitat type using data collected from individuals tracked using radio-telemetry. We calculated the percentage of each insect order available by multiplying the percentage of time that radio-tracked individuals spent in each habitat type by the proportion of each insect order in that habitat type (Whitaker, 1994).

We tested for differences in the availability of each insect order and the relative abundance of each insect order in fecal pellets among the four stages of reproduction using a one-way analysis-of-variance (ANOVA). For all significant tests, we determined which means differed using Tukey's multiple range test (SAS Institute Inc., 1990). The distribution of all data was determined using the Shapiro-Wilks test (SAS Institute Inc., 1990). All proportional data were transformed prior to analysis using an arcsine, square-root transformation. We used a Studentized t-test to test for differences between the proportion of each insect order in the fecal pellets to the proportion of each insect order available during each stage of reproduction. We used $P = 0.05$ as the rejection criterion for all statistical tests.

RESULTS—A total of 3,842 insects collected from the light traps was identified to the ordinal level. Nine insect orders were identified: Blattodea, Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Mecoptera, and Plecoptera. During all four reproductive periods, >95% of available insects were members of four insect orders: Coleoptera, Diptera, Hymenoptera, and Lepidoptera. The availability of three insect orders differed significantly among the four reproductive periods ($P = 0.011$, Fig. 1). Lepidopterans decreased in abundance from pre-parturition to late lactation. Conversely, coleopterans increased in abundance from pre-parturition to late lactation ($P = 0.030$). The availability of dipterans also differed among the reproductive periods, increasing during parturition and early lactation and decreasing in late lactation ($P = 0.030$).

Fecal pellets contained only insects from the four most abundant insect orders: Coleoptera, Diptera, Hymenoptera, and Lepidoptera. Big brown bats consumed significantly more coleopterans during late lactation than during parturition and early lactation ($P = 0.047$, Fig. 2). Because of this difference and differences in insect availability among the four reproductive periods, data could not be pooled from the four reproductive periods. We analyzed data from each reproductive period separately.

The proportion of insect orders consumed differed significantly from the proportion of insects available during all reproductive periods. During pre-parturition, coleopterans made up 18% of available prey but constituted 81% of insects ingested. Lepidopterans, dipterans, mecopterans, blattodeans, and hemipterans were available in higher concentrations than were ingested (Table 1). During the period of parturition, Coleoptera made up 17% of the available prey but constituted 77% of insects ingested. Lepidopterans, dipterans, and hemipterans were available in higher concentrations than were

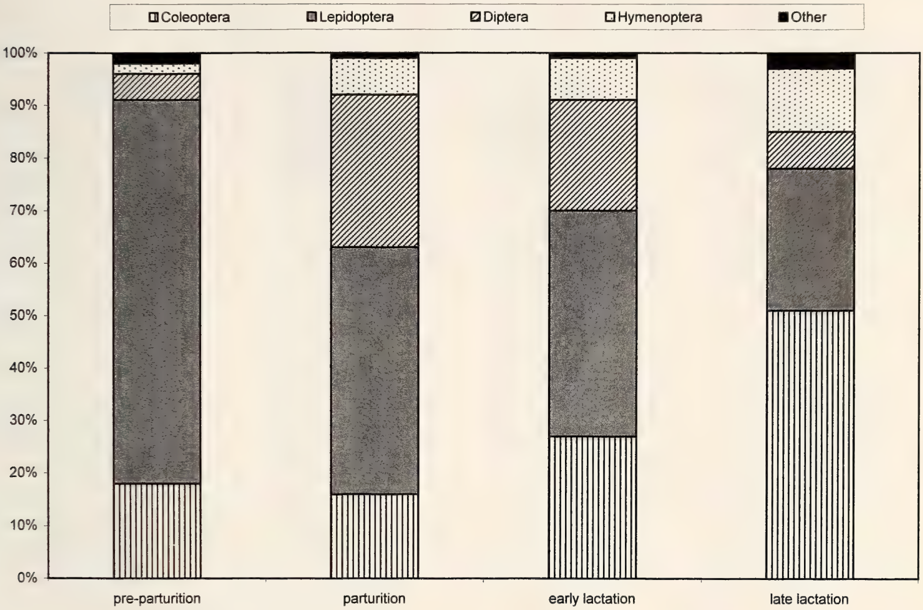

FIG. 1. The relative abundance of insects in foraging areas used by a maternity colony of big brown bats in Clarke Co., Georgia, during four stages of reproduction: pre-parturition, parturition, early lactation, and late lactation.

ingested (Table 1). Only 27% of available prey during early lactation were coleopterans. However, 77% of insects ingested during this stage were coleopterans (Table 2). Lepidopterans, dipterans, homopterans, blattodeans, hemipterans, and plecopterans were available in higher concentrations than they were ingested (Table 2). During late lactation, coleopterans made up 51% of available insect prey but constituted 90% of insects ingested. Lepidopterans, dipterans, hymenopterans, homopterans, blattodeans, and hemipterans were available in higher concentrations than they were ingested.

During each of the four stages of reproduction, big brown bats selected coleopterans and avoided dipterans, hemipterans, and lepidopterans (Fig. 3). Members of the other insect orders were taken in proportion to their abundance in the environment (i.e., hymenopterans) or were found infrequently (e.g., blattodeans and homopterans).

DISCUSSION—The diet of the big brown bats we examined was similar in some respects to the diet of big brown bats in other regions of the United States, but it differed in others. The most common (X = 81%) prey of the bats that we examined consisted of coleopterans throughout the reproductive period. Big brown bats often are described as "beetle specialists" (Black, 1974) because the diet of big brown bats largely consists of coleopterans (Black, 1972, 1974; Hamilton, 1933; Whitaker, 1972, 1995). We found that

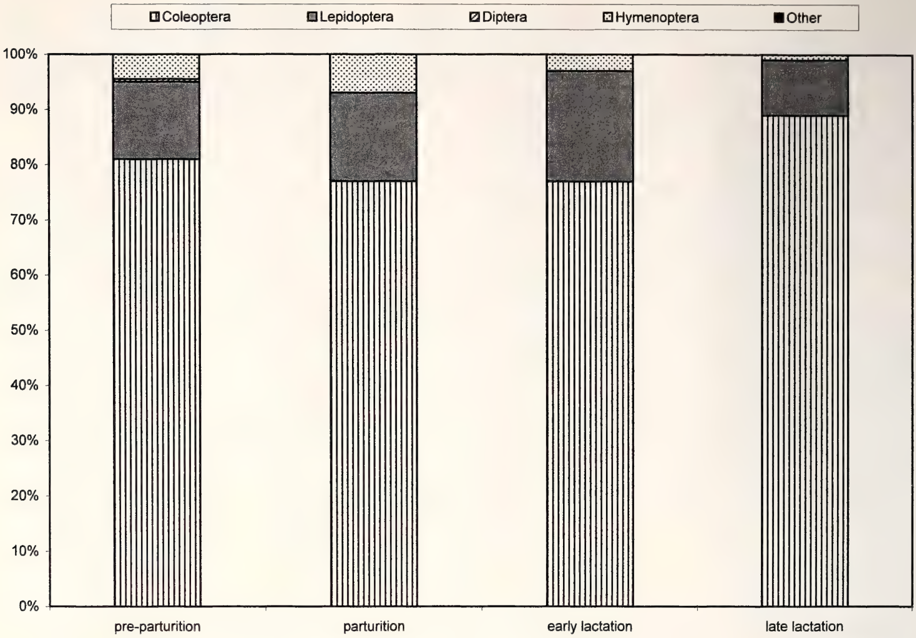

FIG. 2. The relative abundance of insects consumed by a maternity colony of big brown bats in Clarke Co., Georgia, during four stages of reproduction: pre-parturition, parturition, early lactation, and late lactation.

big brown bats in the southeastern United States selectively feed on coleopterans during the period of parturition and lactation.

The amount of lepidopterans consumed differed from previous studies. During May and June, lepidopterans may make up a more significant portion of the diet of big brown bats in the Southeast than in other regions of the United States (Fig. 4). Other than during the period immediately following spring emergence, lepidopterans were not an important dietary component of big brown bats in the colony that Whitaker (1995) studied. Lepidopterans typically are not important components of the diet of big brown bats (Black, 1972; Whitaker, 1972). The proportion of the diet composed of lepidopterans differed significantly among 11 big brown bat colonies examined by Whitaker (1995), however, the maximum proportion of the diet composed of lepidopterans among the colonies was 0.089. The proportion of the diet composed of lepidopterans of the colony that we examined averaged 0.151 and never dropped below 0.098.

Whitaker (1995) found that hemipterans were the second most commonly consumed insect in many big brown bat colonies. Hemipterans rarely were consumed by members of the colony that we examined.

Studies investigating the diet of bats rarely consider temporal shifts in insect availability or foraging selectivity (Whitaker, 1995). We found that the proportion of three insect orders available and the proportion of one

TABLE 1. The relative abundance of each insect order available compared to the relative abundance of each insect order consumed by a maternity colony of big brown bats during pre-parturition and parturition in Athens, Clarke Co. Georgia, 1998.

	Pre-parturition				Parturition			
	Available		Fecal		Available		Fecal	
Insect orders	X	SE	X	SE	X	SE	X	SE
Major orders[a]								
Coleoptera	0.180*	0.023	0.812*	0.146	0.165*	0.035	0.767*	0.039
Diptera	0.050*	0.010	0.005*	0.002	0.295*	0.025	0.002*	0.002
Hymenoptera	0.020	0.010	0.048	0.024	0.066	0.054	0.070	0.031
Lepidoptera	0.730*	0.033	0.140*	0.102	0.470*	0.004	0.161*	0.039
Minor orders[b]								
Blattodea	0.010*	0.005	0.000*	0.000	0.000	0.000	0.000	0.000
Hemiptera	0.005*	0.005	0.000*	0.000	0.004*	0.002	0.000*	0.000
Homoptera	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mecoptera	0.005*	0.005	0.000*	0.000	0.000	0.000	0.000	0.000
Plecoptera	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

[a] Major orders = insect orders whose available relative abundance was $> 1\%$ during all four stages of reproduction.

[b] Minor order = insect orders whose available relative abundance was $\leq 1\%$ during all four stages of reproduction.

* indicates significant difference ($P \leq 0.05$) between proportion available and consumed.

TABLE 2. The relative abundance of each insect order available compared to the relative abundance of each insect order consumed by a maternity colony of big brown bats during early and late lactation in Athens, Clarke Co. Georgia, 1998.

	Early lactation				Late lactation			
	Available		Fecal		Available		Fecal	
Insect orders	X	SE	X	SE	X	SE	X	SE
Major order[a]								
Coleoptera	0.270*	0.010	0.767*	0.041	0.510*	0.090	0.895*	0.023
Diptera	0.210*	0.020	0.000*	0.000	0.050*	0.050	0.000*	0.000
Hymenoptera	0.081	0.051	0.032	0.025	0.119*	0.071	0.007*	0.007
Lepidoptera	0.434*	0.066	0.203*	0.042	0.274*	0.057	0.098*	0.024
Minor orders[b]								
Blattodea	0.001*	0.001	0.000*	0.000	0.001*	0.001	0.000*	0.000
Hemiptera	0.001*	0.001	0.000*	0.000	0.021*	0.016	0.000*	0.000
Homoptera	0.002*	0.002	0.000*	0.000	0.004*	0.004	0.000*	0.000
Mecoptera	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Plecoptera	0.001*	0.001	0.000*	0.000	0.000	0.000	0.000	0.000

[a] Major orders = insect orders whose available relative abundance was > 1% during all four stages of reproduction.

[b] Minor order = insect orders whose available relative abundance was ≤ 1% during all four stages of reproduction.

* indicates significant difference ($P \leq 0.05$) between proportion available and consumed.

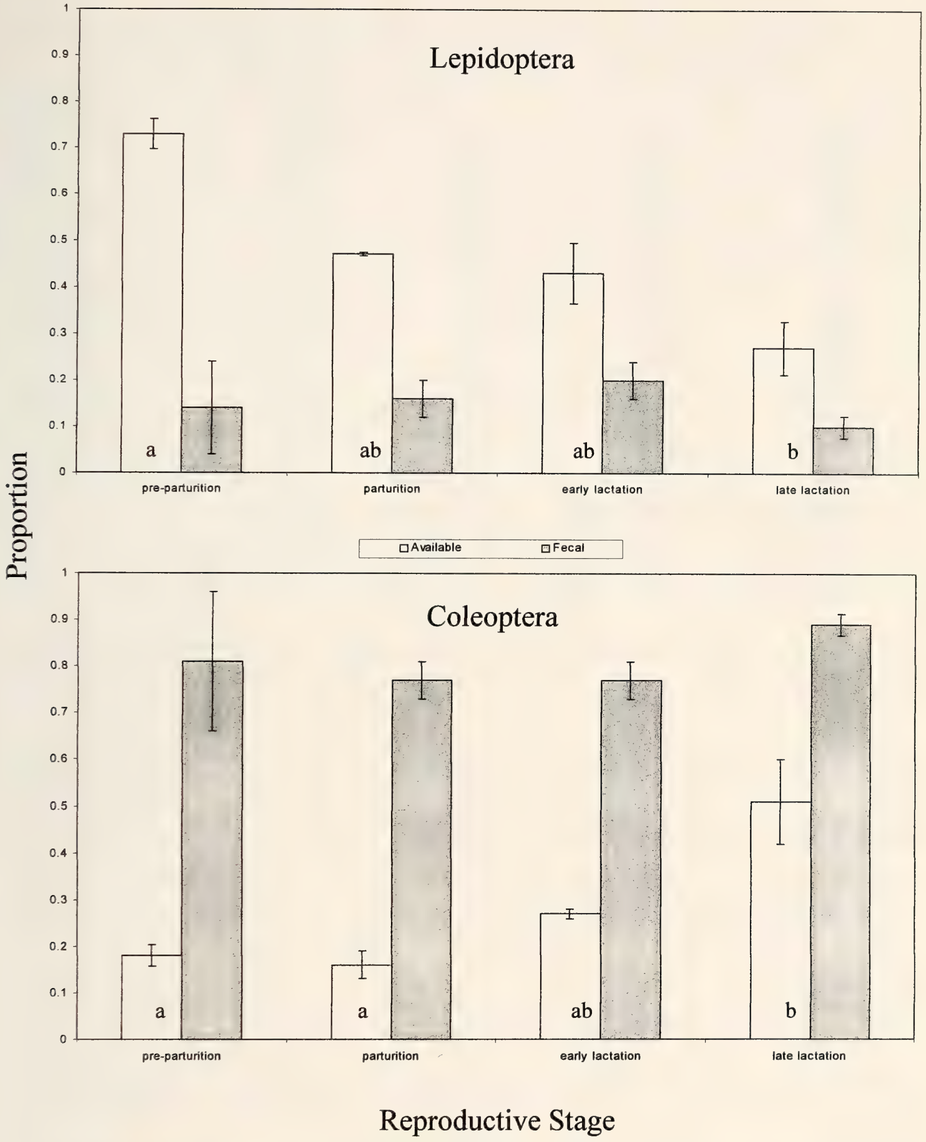

FIG. 3. A comparison of the proportion of lepidopterans and coleopterans in foraging areas and in the diet of a maternity colony of big brown bats in Clarke Co., Georgia, during four stages of reproduction: pre-parturition, parturition, early lactation, and late lactation.

insect order consumed differed during different stages of reproduction. Despite significant shifts in the proportions of insect orders available, the proportion of each insect order in the diet remained relatively unchanged (Fig. 3). The foraging preferences of big brown bats may be unaffected by significant fluctuations in insect availability.

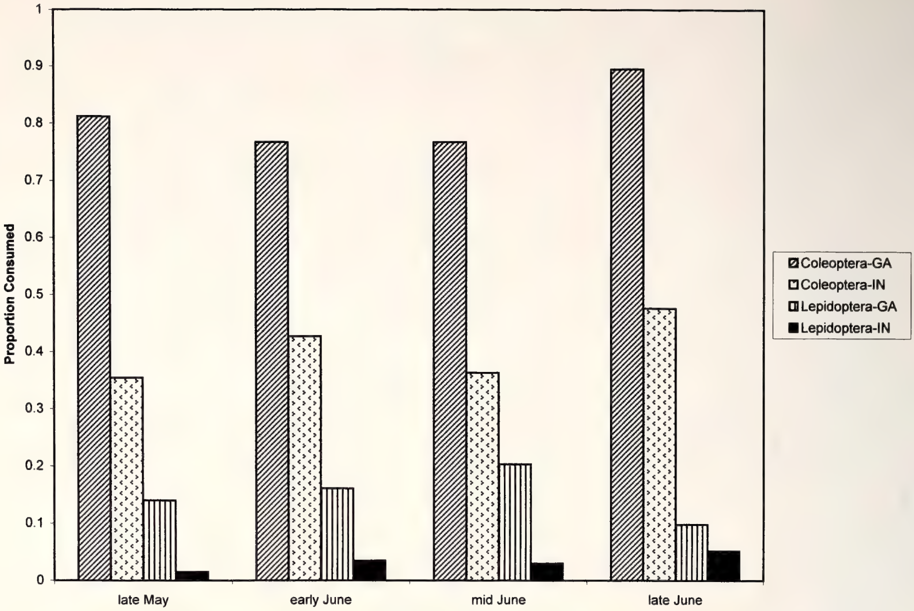

FIG. 4. A comparison of the proportion of diet composed of coleopterans and lepidopterans between a maternity colony of big brown bats in Vigo Co., Indiana and Clarke Co., Georgia.

CONCLUSIONS—The composition of available insect communities and energetic demands can change significantly over relatively short periods (five weeks in this study). These differences may result in temporal shifts in the foraging patterns and diet of bats and should be considered when investigating foraging behavior. Future emphasis should be placed on documenting shifts in diet that occur during periods of reproductive activity and while bats are preparing for hibernation. These also are the periods during which efficient foraging is critical because of increased energy demands. Information concerning the diet of bats during these periods can be used by land managers to predict the impact of land management activities on the food supply of neighboring bat populations during these periods of high-energy demands.

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BIOLOGY AND ECOLOGY OF *RIVULUS MARMORATUS*: NEW INSIGHTS AND A REVIEW

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Abstract: *Rivulus marmoratus* (Pisces: Aplocheilidae) is a small cyprinodontid indigenous to mangroves of the western tropical Atlantic. This species is well known as the only self-fertilizing, hermaphroditic vertebrate, and populations normally consist of genetically diverse groups of homozygous clones. However, male fish are known from a few populations, and outcrossing and heterozygosity have been documented from two areas in Central America. *Rivulus marmoratus* also exhibits a number of behaviors and environmental tolerances unusual in fishes, and since the species is secretive, rare in some habitats and difficult to collect, knowledge of its natural history has been limited until recently. Within the last decade field and laboratory work and ongoing investigations into *R. marmoratus* genetics have added greatly to our knowledge of this unusual fish. This study provides a general review of the biology and ecology of *R. marmoratus*.

Systematics/Nomenclature—*Rivulus marmoratus* (Poey) (common name: mangrove rivulus) is a small, cryptic, Neotropical cyprinodontid fish inhabiting mangrove marshes over a vast range of the shoreline of the western Atlantic, Caribbean and Gulf of Mexico. The fish has attracted considerable scientific attention in the last three decades due to its unique reproductive mode as a self-fertilizing hermaphrodite, its restriction to the fringes of marsh habitat and the impact of these traits on the evolution and population genetics of the species. The type locality of *R. marmoratus* is Cuba, although in the original description by Poey in 1880 there is some confusion that the specimen may have come from the United States. Synonyms listed include: *R. ocellatus* Hensel, *R. heyei* Nichols, *R. marmoratus bonairensis* Hoedeman. Of these, *R. ocellatus* has been widely used, but a 1992 decision by the International Commission on Zoological Nomenclature (Case #2722) has conserved the specific name *R. marmoratus* and synonymized *R. ocellatus*.

General Description—In body form, *R. marmoratus* generally resembles cyprinodonts of the genus *Fundulus*, one of the main differences being that *R. marmoratus* has tubular anterior nares. The body is elongate, slender and dorso-ventrally flattened. Both dorsal and anal fins are set well back, and the caudal fin is rounded. Body coloration of hermaphrodites is an overall dark brown or maroon, but wild specimens may vary in degree of dark coloration depending upon the substrate background color. A distinctive "rivulus spot" or ocellus is found at the upper part of the caudal peduncle base. The sides of the body have small black "pepper" spots against a reticulated background. A dark humeral spot is found at the base of the pectoral fin (Figure 1). Male fish, which are found in some populations, lack an ocellus and also have a varying sheen of red/orange/yellow to the flanks and posterior fins. The anal, caudal and sometimes dorsal fin tips may be darkly pigmented in males (Figure 2). The largest specimen collected in Florida was 62 mm SL and 56 mm SL in Belize, but most individuals range from 20–40 mm TL (unpub. data).

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OVERALL GEOGRAPHIC RANGE—*Rivulus marmoratus* is found in the subtropical/tropical western Atlantic/Caribbean basin, from southeastern Brazil north through the Greater and Lesser Antilles, Venezuela through Central America at least to the Yucatan and both coasts of central Florida (Davis et al., 1990; Taylor and Snelson, 1992). Although collections from Brazil north to Guiana are non-existent, it is likely that the range of the fish is contiguous through this area. In Florida, the species is now confirmed on the west coast north to Tampa Bay and on the east coast north to Melbourne Beach (Brevard County). However, an apparent "outlier" population from Volusia County south of New Symrna Beach has also been documented (Taylor, 1999a).

Rivulus marmoratus has the widest range of the 70 well defined (plus about 30 uncertain) species in the genus *Rivulus* (Huber, 1992) and is the only marine species other than *Rivulus caudomarginatus. Rivulus caudomarginatus* is sympatric with *R. marmoratus* in the mangroves of southeastern Brazil (Huber, 1992; Lazara, 1998).

COLLECTIONS—Prior to the late 1980s, reported collections of *R. marmoratus* in non-U.S.A. waters generally numbered less than 10 individuals per collection, and collection of this species was generally an incidental occurrence in fish surveys of the mangal (mangrove ecosystems). An exception to this was in Grand Cayman, B.W.I., where over 500 individuals were collected over a 7-year period in the 1970s, during a study of fishes preying on mosquito larvae in the mangrove swamps (Todd and Giglioli, 1983).

Until the field studies of Davis and coworkers (1990), few ichthyologists specifically pursued the collection of *R. marmoratus.* Davis and colleagues have since collected several hundred specimens from the Belize barrier reef cays (Davis et al., 1990; Taylor, 1999a). In addition, within the last few years, 94 specimens have been taken from the Bay Islands, Honduras and 78 specimens from Exuma, Bahamas (Taylor, 1999b). Taylor (1999a) has cataloged known collections from Florida and estimates that 2,188 individuals have been taken since 1928. Now that the distinct microhabitat requirements for *R. marmoratus* have been identified (crab burrows, intermittently

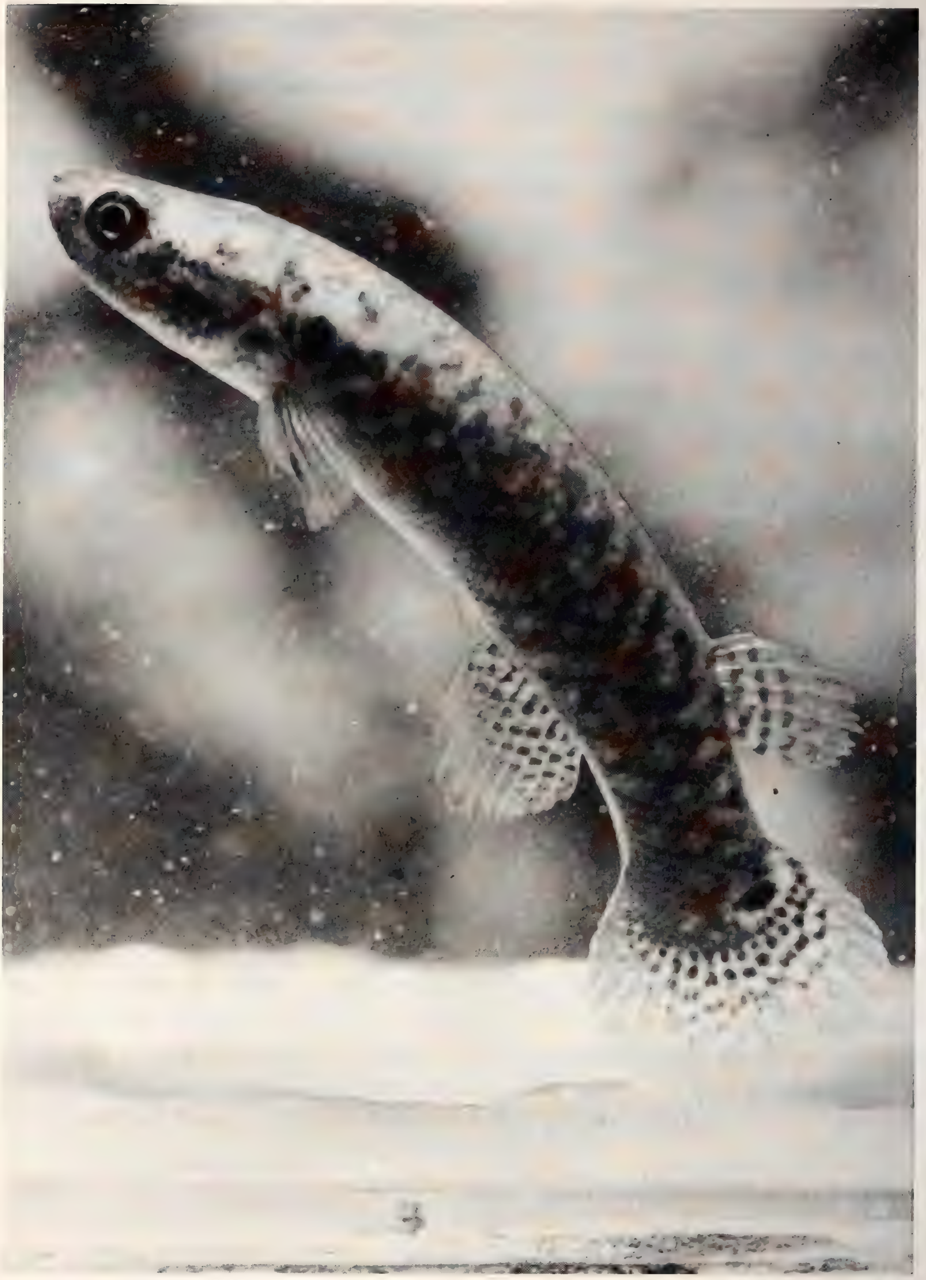

FIG. 1. Hermaphrodite of *Rivulus marmoratus* from Belize, C. A. (SL about 35 mm).

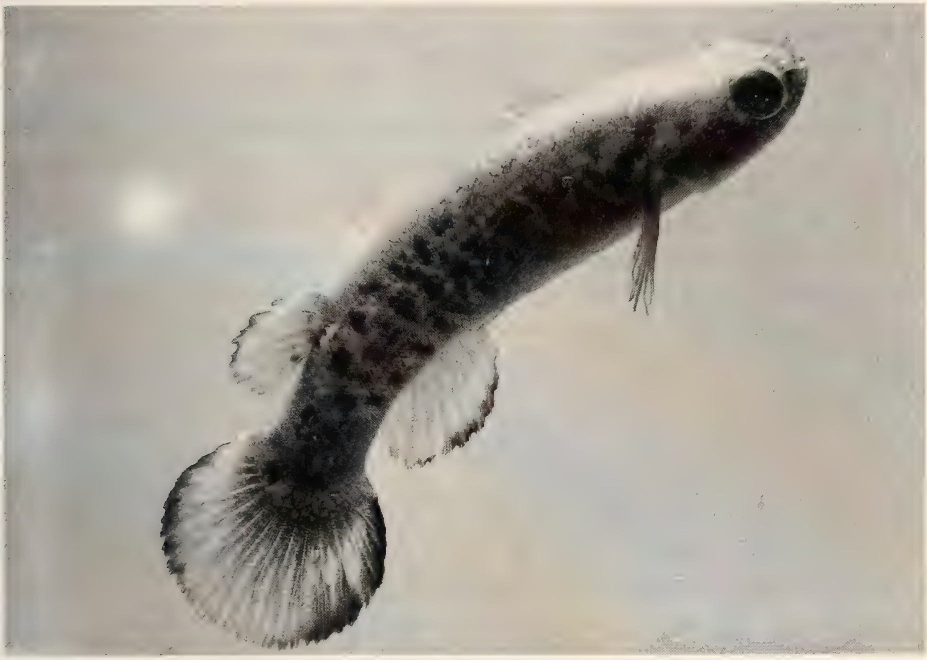

FIG. 2. Male *Rivulus marmoratus* from Belize, C. A. (SL about 35 mm).

dry and stagnant mangrove pools), it can be anticipated that collections throughout the fish's range will increase.

ECOLOGY—*Habitat preferences*—*Rivulus marmoratus* have been collected within broadly defined categories of microhabitats within the mangal: crab burrows, stagnant pools, sloughs or ditches (often intermittently dry) and some fossorial niches (inside or under damp logs, debris, leaf litter, etc.). They have also been reported from cave systems and solution holes adjacent to mangroves in the Bahamas (Gerace, 1988; Taylor, 1999a). Davis and coworkers (1995) pointed out that *R. marmoratus* is one of only two (the other being *Gambusia rhizophorae*) truly "mangrove dependent" fish species, in which the entire life cycle is completed in the mangal. In fact, the range of *R. marmoratus* coincides with that of the red mangrove (*Rhizophora mangle*), and parallels may be drawn between physiological and ecological tolerances of fish and plant (Davis et al., 1995). Carole McIvor (cited as pers. comm. in Davis et al., 1995) reports that among a suite of fishes examined, *R. marmoratus* exhibits the "strongest" C/N/S mangrove stable isotope signal, reflecting its dietary association with the primary productivity of mangrove systems. However, in spite of its almost "benthic" character, on two occasions *R. marmoratus* has been collected in channel nets set in heavy tidal flow, adjacent to mangrove habitat. Roessler (1970) took a single specimen in a Florida Everglades mangrove canal system, and two juvenile specimens (~ 7–9 mm) were taken in a tidal creek near Naples, FL 100 m from the nearest mangroves (Peters, 1998).

Water quality—It has often been noted that *R. marmoratus* can tolerate adverse water quality conditions that may be fatal to other fishes (Kristensen, 1970; Abel et al., 1987; Taylor, 1990), and it is frequently the only species collected in the microhabitat it occupies (Taylor et al., 1995). In mangrove systems, *R. marmoratus* have been collected at salinities ranging from 0–68 ppt (Taylor et al., 1995), and in the laboratory juveniles remained viable at 70–80 ppt (unpub. data). Collections at low salinity conditions in mangroves are generally temporary conditions following heavy rainfall. *Rivulus marmoratus* can be reared and will reproduce at very low salinity (e.g. 1 ppt) but matures at a slower rate and at a greater size (Lin and Dunson, 1995). Fish reared at 12 and 40 ppt had greater mass than those of equivalent age reared at 1 ppt (Lin and Dunson, 1999). However, several attempts to introduce *R. marmoratus* to freshwater habitats in Florida have not been successful, except in one instance where no other fish species were present and the habitat was intermittently dry (Taylor, 1999a).

Temperature—*Rivulus marmoratus* have been collected at temperatures from 7–38° C (Taylor et al., 1995), and the fish can survive temperatures as low as 5° C when emersed (Taylor, 1999a). Huehner and coworkers (1985) demonstrated that *R. marmoratus* in laboratory aquaria/terraria will leave the water (emerse) as temperatures decrease toward 19–20° C. In mangrove pools on the east coast of Florida artificially stocked with *R. marmoratus* (Taylor et al., 1995), the fish have been found inside termite galleries of rotting logs at the water's edge, but out of the water (Taylor, 1999a). Similar behavior was previously observed in drying mangrove pools in Belize, C.A. (Davis, 1991).

As are most tropical species which range north into sub-tropical/temperate climes, *R. marmoratus* are vulnerable to extreme cold events (Taylor, 1993), which presumably limit their northern distribution. Their utilization of fossorial habitats (such as crab burrows), which may offer some thermal buffering, allows the fish to establish a range north of areas where open water temperatures would otherwise prove lethal (Taylor, 1992).

Emersion—*Hydrogen sulfide/anoxia*—Hydrogen sulfide (H_2S) is a ubiquitous component of the mangal and, as a potent toxin, challenges any fish life present (Davis et al., 1995). In the field, *R. marmoratus* is frequently seen with a patchy white coating on the body and fins, which may either be a mucus response to adverse water quality (Davis et al., 1990) or the actual growth of sulfur-oxidizing bacteria on the epidermis (unpub. data). *Rivulus marmoratus* avoids intolerable levels of H_2S through a behavior known as emersion, or the act of leaving the water and residing in damp substrates (Abel et al., 1987; Taylor, 1990). Kristensen (1970) was the first to describe emersion in *R. marmoratus,* and the behavior has been well-documented in this species and in many congeners (Huber, 1992). Factors other than high levels of H_2S (e.g. intra-specific aggression or escape) may also induce this behavior (Taylor, 1988). Fish can survive at least 66 d out of the water in damp substrates, and they resume feeding immediately upon reflooding (Taylor, 1990). While emersed, *R. marmoratus* respires with a network of expanded capillaries in the skin and fins (Grizzle and Thiyagarajah, 1987), but the overall physiology of the process has not been investigated. Elevated H_2S is associated with depleted oxygen, and the interaction of these two factors in the induction of emersion is unknown. If *R. marmoratus* are captured in traps which are completely submerged in high H_2S environments, the fish frequently die. Contact with the air-water interface, allowing skin respiration, may be obligatory under these circumstances (Davis et al., 1990).

In the field, emersed fish will often aggregate, presumably to retain moisture, and in this regard one is reminded of salamanders or other amphibians (Taylor, 1999a). Generally, emersed fish are quiescent, and the intra-specific aggression which is common in aquaria is curtailed. A further parallel to the amphibian analogy is that emersion can also be an active event (Taylor, 1990), in which *R. marmoratus* travels over damp substrates by serpentine wiggling or flipping. Such "overland" excursions reveal a well-developed local knowledge of terrain (Taylor, 1990), and fish dropped during field collection frequently flip directly into a refuge (crab burrow, etc.) (pers. obs.). *Rivulus marmoratus* will leap from the water to capture prey, but prey so captured are consumed in the water (Huehner et al., 1985; Taylor, 1990).

DIET—*Rivulus marmoratus* is a predator, and a variety of invertebrates (terrestrial and aquatic) form the bulk of the diet (Harrington and Rivas, 1958; Huehner et al., 1985; Taylor, 1992). Fish scales have also been found in the gut, and the species is known to be cannibalistic (Kristensen, 1970; Taylor, 1988) and will eat its own eggs in captivity (Davis, 1986). Taylor (1992) found that 60% of the fish collected from land crab burrows had empty guts, and this relative infrequency of feeding is likely in other marginal, intermittently dry habitats where the fish is found. Periods of mangal flooding probably allow *R. marmoratus* the opportunity to feed heavily prior to the arrival of other fishes which may be migrating from nearby permanent sources of water (e.g. permanent ponds, estuarine water). Heavy feeding during flood cycles may give *R. marmoratus* the nutritional reserves to survive during drought or low water conditions. *Rivulus marmoratus* is an effective mosquito larvivore, and in the laboratory fish of 40 mm SL ate up to 80, 4th-instar saltmarsh mosquito larvae in 24 h. One-day old *R. marmoratus* also ate up to 21, 1st-instar saltmarsh mosquito larvae in 24 h (Taylor et al., 1992).

GROWTH—In the laboratory, fish reared at 25° C reached 19–21 mm SL at age 90 d. In a more variable temperature regime (21–29° C) juveniles reached 18 mm SL at age 90 d and 22 mm SL by age 200 d (Taylor, 1999a). Koenig and Chasar (1984) found growth rates at 25° C of 18 mm TL at age 90 d and 26 mm TL at age 200 d. However, feeding regimes and ambient salinity varied in all of these studies. Lin and Dunson (1995) reported hermaphrodites reared at 26° C under a high food regime reached 27 mm TL at age 90 d and under low food, 25 mm TL at age 125 d. In the laboratory, offspring of parents fed under low food regimes had a faster growth rate (length and mass) than offspring of parents from high food regimes (Lin and Dunson, 1999). Males are significantly smaller than hermaphrodites of the same age when both were reared under high food regimes (Lin, 1993). Adult fish may live up to 5 y in captivity, and males live longer in captivity than hermaphrodites (Taylor, 1999a). Sexual maturity in hermaphrodites is generally given as occurring at age 90 d (Kristensen, 1970; pers. obs.). There are limited data on growth rates in the wild. Dunson and Dunson (1999) found that juvenile *R. marmoratus* (body mass 6–42 mg wet weight; age/length not given) placed into cages in Florida west coast mangroves grew at a maximum of 3.5–4.0% daily (body mass).

REPRODUCTION—*Rivulus marmoratus* is the only vertebrate known to generally reproduce as a homozygous, self-fertilizing hermaphrodite. Thus, the fish essentially "clones" itself. The gonad in hermaphrodites is a bilobed ovotestis. The gonad appears ovarian but contains both oogenic and spermatogenic tissues which are undifferentiated by membranes (Harrington, 1961; Soto et al., 1992). Kweon and coworkers (1998) examined the ultrastructure of *R. marmoratus* spermatozoa and report that they are of a primitive type, resembling those of externally fertilizing teleosts. This suggests a recent shift to internal self-fertilization. Mature spermatozoa are found in ducts throughout the organ, and fertilization takes place within these ducts at the time of ovulation. Fertilized eggs can be held within the ducts for up to 77 h, but 80% are released within 24 h (Harrington, 1963).

Internal self-fertilization is very efficient in *R. marmoratus,* but on occasion some unfertilized eggs are emitted, an important factor in the possibility of outcrossing (Harrington, 1971)(see below). The physiological/hormonal mechanisms by which the two germ tissues in the ovotestis function in such close proximity are quite fascinating and completely unknown. Cole and Noakes (1997) report that in lab-reared, young (<100 d from hatching) *R. marmoratus,* "pure" females (e.g. only ovarian tissue present) dominate, and subsequent to age 100 d, hermaphrodites dominate. This argument for "pure" females, however, is based on histological work on lab-reared fish, and wild fish have not been examined in such detail. Sexuality and sex expression in lab-reared *R. marmoratus* are highly variable (pers. obs.), and conclusions based on laboratory studies may not necessarily apply to wild populations.

In captivity, adult hermaphrodites will lay up to 8 fertile eggs/day (Taylor et al., 1992), but the norm is closer to 1 egg/day (Harrington, 1963; Koenig and Chasar, 1984). Freshly captured, wild hermaphrodites have been extremely gravid on occasion, and one specimen released more than 50 viable eggs of varied developmental stages shortly after capture (Taylor, 1999a). This observation suggests that "mass" egg deposition by a single individual may sometimes occur in the wild. Eggs range from 1.5–2.0 mm in diameter and have a clear, rubbery chorion. Most eggs hatch within 16 d of fertilization, but some may take an additional 2 weeks or more (Koenig and Chasar, 1984). Fertile eggs will develop if incubated under only damp conditions (without standing water), and once development is complete, they hatch spontaneously upon flooding (pers. obs.). Ritchie and Davis (1986) report circumstantial evidence of embyronic diapause in wild *R. marmoratus,* where larval fish appeared in pools after the mangal had dried and reflooded.

Although few eggs have been found in the wild, the limited data suggest that this species may strand its eggs, a trait shared with several congeners. A single egg has been found out of the water on the sides of a crab burrow (Taylor, 1990), and several eggs were found in leaf litter above the water line at the edge of a mangrove pool (Taylor, 1999a). In a crab burrow "microcosm", *R. marmoratus* consistently laid eggs out of the water and generally at night (Taylor, 1990).

Taylor (1992) examined the gross state of gonads from 111 *R. marmoratus* captured during Feb.–May from crab burrows in east central Florida. Fish varied in SL from 14–48 mm ($\bar{x}$ = 25.2 mm). Only three fish (20–25 mm SL) contained no developing eggs. The remaining 108 fish all contained either developing or mature eggs (>1 mm dia). Early in the collection period (Feb.) eggs were smaller (<0.25 mm dia) and fewer in number (40–60 total). Later collections (April–May) had larger eggs (>1 mm dia) and greater numbers (up to 75 total) in the ovotestis.

Juveniles (i.e. < 10 mm) have rarely been collected in the wild. Harrington and Rivas (1958) took 22 small fish (7.5–11.1 mm SL) in August, and about a dozen fish in the range of 7–15 mm SL have been taken in the fall and early winter from east-central Florida (Taylor, 1999a).

GENETICS—Harrington and colleagues identified three clones from wild fish collections: "DS" and "NA" from Vero Beach, Florida and "M" from Miami, Florida (Kallman and Harrington, 1964; Harrington, 1975). These three clones and a suite of other wild-caught fish from Florida were indistinguishable from each other by allozyme comparisons (Massaro et al., 1975), and an ordinarily hypervariable region of the mtDNA "D" loop is also nearly uniform (Turner, 1996). Through more sensitive DNA fingerprinting, both Turner and coworkers (1990, 1992a) and Laughlin (1993) have determined that in populations from both Florida and Belize, the ratio of distinguishable genotypes (clones) to individuals was nearly 1:1, i.e. each fish represents a discrete genetic clone. Such a level of genetic variability approaches that of sexually reproducing populations and has not been documented among other clonal animals. Only certain clonal grasses exhibit this level of diversity (Turner et al., 1992a).

Weibel and coworkers (1999) surveyed mtDNA in *R. marmoratus* from Brazil, Bahamas (Turks and Caicos), several Florida locations and Belize. They found that Florida and Belize clones were phyletically indistinguishable and more closely related to each other than to the Bahamas/Brazil lines. In addition, the Florida/Belize fish shared a common ancestor of more recent origin than did Brazil/Bahamas. Thus, eastern and western Caribbean lineages were identified.

Little chromosomal variation in number (2N = 48) or morphology was found in a cytogenetic analysis of *R. marmoratus* from Brazil to Florida. This finding was deemed somewhat remarkable since other aplocheiloids and some congeners had considerably more variation. One explanation presented is that *R. marmoratus* is of relatively "recent" origin and has spread over such a wide range because of its superior colonizing ability (Sola et al., 1997).

Although *R. marmoratus* typically contain functional ovotestes and internally self-fertilize, the occasional presence of fish that are completely male complicates the pattern of clonal reproduction reported for this species. Harrington (1967) first identified this deviation from the hermaphroditic character in laboratory specimens reared at low temperature (20°C), and later reported the first wild male specimen, found in south Florida (Harrington and Kallman, 1968). In addition, Harrington (1971) also transformed young hermaphrodites into "secondary" males by early rearing them at high temperature (30° C). Lin (1993) found that production of males in the laboratory varied across clones, and the highest male production was not always associated with lower rearing temperatures (19° C) and hypothesized that the lower threshold temperature for male induction will be lower at high latitudes and higher at low latitudes. Fisher (1997) also found male production variation among clones under three rearing temperatures (19, 22.5 and 26° C), but his findings generally confirmed those of Harrington (1967), with greater incidence of males at lower temperatures. He was not, however, able to demonstrate that clones originating from more southerly locales had a higher low-temperature threshold of male induction, or correspondingly, that more northerly clones had a lower induction temperature. Davis and coworkers (1995) suggested that in addition to environmental factors known to occasionally produce males (i.e. both high and low temperature), ecological or habitat disturbance may also result in male production. Taylor and coworkers (1995) speculate that other factors, possibly "social" factors, may be involved in the induction of males. A mangrove pond in east-central Florida artificially stocked with *R. marmoratus* produced high densities of fish, and males were present where they were otherwise unknown in natural habitats (Taylor et al., 1992). Fewer than 15 wild males have been reported from Florida, all from the southeast or southwest and west coasts and the Florida Keys (Davis et al., 1990; Taylor, 1999a). Kristensen (1970) also identified male fish from Curacao, Netherlands Antilles, although more recent collections from there have not included male fish (Lubinski et al., 1995). The widespread occurrence of apparently sexually competent male fish from some cays in Belize, Central America, has also been reported (Davis et al., 1990; Turner et al., 1992a). The Belize cays males comprise from 10–25% of the population and are presumably involved in sexual reproduction with hermaphrodites, as evidenced by the high incidence of heterozygosity on some cays (Lubinski et al., 1995). Heterozygosity is still the norm in this habitat after several years, as determined from recent DNA fingerprinting (Taylor, 1999b). Two males are also known from a collection (n = 94 individuals) from Utila, Bay Islands, Honduras, and one was found in a collection of 78 individuals from Norman's Pond Cay, Exuma, Bahamas (Taylor, 1999b). A limited DNA fingerprint sample from the Honduras population revealed a low percentage of heterozygosity (2%) while the Bahamas fish were uniformly homozygous (Taylor, 1999b). These data may therefore suggest that a threshold of male fish abundance may be required for outcrossing to take place. No male fish, however, have been reported from the considerable range encompassing the northern and eastern coasts of South America to southern Brazil, although few collections are known from here.

The clonal pattern of inheritance and homozygosity was first reported in Florida *R. marmoratus* by Kallman and Harrington (1964), and these observations were confirmed with later fin and organ transplant experiments (Harrington and Kallman, 1968). More recently, clonality and homozygosity has been confirmed by multilocus DNA fingerprinting (Turner et al., 1990; Laughlin et al., 1995), in which fingerprints of F1 progeny from wild-caught individuals are compared with each other or with parental fingerprints. Fingerprints of various wild-caught Florida *R. marmoratus* reveal that many clones are present (i.e. 1 fish/1 clone) with very little clonal "overlap", and most fingerprints are separated by multiple mutations. Clonal diversity in *R. marmoratus* also may vary temporally. At two south Florida sites, there was no detectable clonal overlap in four small samples (n = 34 fish) collected one and three years apart (Turner et al., 1992b). Mutation rates alone are not sufficient to explain such turnover, but mutation combined with high migration rates from individuals from different lineages are a reasonable explanation. Laughlin (1993) compared fingerprint bands of 16 specimens from Indian River Lagoon, Florida and 12 from the Everglades region and found that there was 23% more band sharing within populations than among populations. He concluded that migration between populations may not be as important as previously estimated and that high clonal diversity may be a result of natural selection acting at the molecular DNA level. However, in a later publication Laughlin and coworkers (1995) suggested that observed clonal diversity and turnover could not be explained by mutation and is the result of migration only.

The significance of this great clonal diversity is still unknown. Among the three Harrington/Kallman clones first identified, differences were found in age at sexual maturity, extent of sex change at senescence, incidence of low-temperature male induction and temperature induced meristic variation (Harrington, 1971; Harrington and Crossman, 1976). Fisher (1997) also found differences in low-temperature induction of males and in incidence of morphological anomalies among seven different clones originating from Florida to Brazil. Lin and Dunson (1995) found among five clones (from Florida, Yucatan and Belize) that reproductive fitness was affected differently in the different lines by variation in food level and salinity. Lin and Dunson (1993) report that individual clones had different tolerances to toxic heavy metal exposure. Existing information on clonal distribution of this widely distributed fish is present for only two populations: Belize and Florida. Some very preliminary data may indicate that the ratio of individuals/clone increases on a south-north cline, that is, there may be less clonal diversity at the northern end of the fish's range (Turner et al., 1992b). These data, however, are based on small sample sizes (n = 58 fish) from only five sites, two of which were in the Florida Keys. Kallman and Harrington (1964) confirmed the homozygosity of six wild fish collected from Vero Beach, FL by tissue transplantation tests. In the process, they determined that two of the six individuals collected from adjacent marshes were the same clone (clones DS and NSU). It is unlikely that individual clones (with variation only at mini- and micro-satellite loci) are each uniquely adapted to different ecological conditions (Lubinski et al. 1995). Yet, until a thorough survey of clonal structure is completed across a variety of populations and among sympatric clones, the ecological significance of this diversity is unknown.

Heterozygosity in offspring is presumed to result from male X hermaphrodite matings (Lubinski et al., 1995). How hermaphrodites reduce or inhibit self-fertilization is not known. Harrington and Kallman (1968) paired a hermaphrodite which routinely laid unfertilized eggs with a lab-reared male fish and was able to produce an outcrossed (heterozygous) offspring, as determined by an allograft reaction. Outcrossing could also result if pure "females" occur in the wild and males are present (Cole and Noakes, 1997). Overall, outcrossing may be relatively infrequent and appearance of males in some populations may be intermittent and driven by environmental factors not yet understood (Lubinski et al., 1995) Most importantly, the significance of outcrossing in the genetics of a highly successful, clonal organism is completely unknown.

The last decade has added much to our knowledge of this species, yet clearly *R. marmoratus* presents many opportunities for further research, much of it in the realm of molecular genetics. It is hoped that studies of *R. marmoratus* both in the laboratory and in the field will continue, as the fish has still not been investigated throughout much of its range.

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AN EVALUATION OF MERCURY LEVELS IN SPOTTED SEATROUT, *CYNOSCION NEBULOSUS,* IN TARPON BAY, J.N. "DING" DARLING WILDLIFE REFUGE, SANIBEL, FLORIDA, WITH REFERENCE TO PREVIOUS STUDIES

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Abstract: We captured 30 spotted seatrout, *Cynoscion nebulosus,* from J.N. 'Ding' Darling National Wildlife Refuge in 1998 in order to determine the concentration of mercury in muscle tissue. We compared mercury levels found in this study with mercury levels found in *C. nebulosus* captured in 1990 in the refuge. We also regressed concentration of mercury against specimen wet weight for 1998 data. We found that the average concentration of mercury in *C. nebulosus* (0.235 ppm, wet weight) in 1998 was significantly less than the average in 1990 (0.396 ppm, wet weight). No significant relationship existed between mercury concentration and specimen whole body wet weight. Differences in laboratory procedures and/or reductions in natural or anthropogenic inputs of mercury may have contributed to the reduction in mercury concentrations between the two years.

The spotted seatrout, *Cynoscion nebulosus,* is a species of considerable commercial and recreational importance in Florida. In 1994, the year before a nearshore commercial ban on gill netting was enacted in Florida, over 890,000 pounds of *C. nebulosus* were landed by commercial fishers (Florida Marine Research Institute, unpublished) and over 2.7 million pounds were landed by recreational anglers (National Marine Fisheries Service, unpublished). Particularly in predatory species such as *C. nebulosus,* elevated levels of mercury pose a concern to higher level consumers, including humans. Florida currently issues a public health advisory for consumption of fishes that have exhibited mercury levels greater 0.5 mg/kg (parts per million), tissue wet weight (Florida Department of Health and Rehabilitative Services, 1989). The advisory suggests that when the average concentration of mercury in fish fillets is between 0.5 and 1.5 parts per million (ppm) healthy adults should limit consumption to no more than one 4 ounce (114 g) meal per week.

Through their diet fish bio-concentrate mercury as methyl mercury, an organic form that originates from natural and/or anthropogenic sources. Natural sources include volcanic activity, degassing of the Earth's crust, and marine phytoplankton activity, from which mercury volatilizes to the atmosphere (Eisler, 1987). Human activities that contribute mercury to the environment include combustion of fossil fuels, mining of gold, copper and lead, disposal of batteries and fluorescent lamps, and production of electrical appliances, paper and pharmaceuticals (Eisler, 1987). Worldwide, between

2,000 and 3,000 tons of mercury are deposited into the atmosphere from burning coal and incineration of municipal and industrial waste (National Oceanic and Atmospheric Administration, unpublished). Mainly due to human activities, mercury levels in sediment and other abiotic materials are estimated to have increased up to five times pre-human levels (Eisler, 1987).

The rationale for the present study was to determine whether mercury concentrations of *C. nebulosus* inhabiting waters of the refuge had changed over the course of the decade, and to determine whether average concentrations of mercury in *C. nebulosus* had reached minimum state advisory levels.

METHODS—Field sampling was conducted in Tarpon Bay, which lies within J.N. 'Ding' Darling National Wildlife Refuge. Tarpon Bay is a shallow 13 km^2 embayment that, with the exception of an area with several out-buildings on its south shore, is fringed by red mangrove, *Rhizophora mangle.* Additionally, three species of seagrasses are widely distributed in Tarpon Bay: *Thalassia testudinum, Syringodium filiforme,* and *Halodule wrightii.* In 1999, we found that the salinity in Tarpon Bay ranged from 19 to 38 parts-per- thousand (ppt). Tides are predominantly semi-diurnal (McNulty et al., 1972), with a mean diurnal range of 0.5–1.1 m (Wilzbach et al., 1999).

Using hook and line, we captured 30 *C. nebulosus* between August and December, 1998. Immediately upon capture, fish were placed on ice and returned to the laboratory within two hours. In the laboratory, fish were weighed to the nearest gram and dissected in a stainless steel tray. Fish weights ranged from 186 to 921 g. A tissue sample from each specimen's left dorsolateral musculature was removed, wrapped in aluminum foil, placed in a zip-lock™ plastic bag, and frozen for later analysis of mercury concentration. Tissue samples were placed on DRY ICE™ and shipped to University of Missouri-Rolla (UMR) Center for Environmental Science and Technology for analysis of levels of mercury. UMR employs the 3A preparation procedure for analysis of levels of mercury ion (Hg^{++}) in tissue samples. This procedure does not distinguish between types of mercury (mono- or dimethyl mercury) uptaken by test organisms (Sun, 1999), however the highly volatile dimethyl mercury is generally not persistent in aquatic environments (NOAA, 1999).

Due to unequal and small sample sizes we employed the Mann-Whitney test to statistically compare concentrations of mercury found in *C. nebulosus* we collected in 1998 with concentrations found in 11 *C. nebulosus* collected from the refuge in 1990 (Brim et al., 1994a).

With specimens we collected, we employed least squares regression to examine the relationship between concentration of mercury and whole body wet weight.

RESULTS—We found a mean mercury concentration of 0.235 ppm ($n = 30$, S.D. $= 0.068$) wet weight in *C. nebulosus* collected in our study, significantly less than the mean concentration of 0.396 ppm ($n = 11$, S.D. $= 0.127$) wet weight found in *C. nebulosus* collected in 1990 (Mann-Whitney $U = 282.0$; $p<0.001$). None of the 30 specimens collected in 1998 had a mercury concentration that exceeded the Florida lower-level consumptive advisory of 0.5 ppm wet weight.

Least squares regression indicated that body weight of specimens collected in 1998 did not have a significant relationship with concentration of mercury ($r^2 = 0.017$; $p = 0.492$). The fitted regression equation was:

$$y = 0.2132 + 0.0001 \text{ WW}$$

where y is the dependent variable, mercury concentration wet weight (ppm)

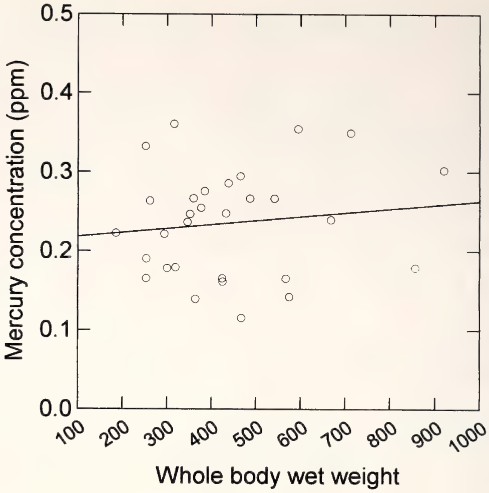

FIG. 1. Result of mercury concentration regressed against whole body wet weight for 30 *C. nebulosus* collected from J.N. 'Ding' Darling National Wildlife Refuge in 1998.

and WW is whole body wet weight. The result of the regression is depicted in Figure 1.

DISCUSSION—Interestingly, we found significantly lower concentrations of mercury in tissue of *C. nebulosus* that we collected in 1998 than in *C. nebulosus* collected by Brim and co-workers (1994a) in 1990 in J.N. 'Ding' Darling National Wildlife Refuge. Our results are similar to a study of mercury contamination in *C. nebulosus* collected from St. Marks National Wildlife Refuge in northwestern Florida in 1991 (Brim et al., 1994b). In that study, mean concentration of mercury in three samples of *C. nebulosus* was 0.19 ppm, 0.30 ppm, and 0.33 ppm, wet weight (n = 7; n = 11; and n = 8, respectively).

Results of regression show that for fish we collected, whole specimen wet weight did not significantly explain variability in mercury concentration. Our results contrast with those of Lange and co-workers (1993). In that study, mercury concentration of largemouth bass (*Micropterus salmoides*) collected from Florida lakes was positively correlated with fish size and fish age and negatively correlated with alkalinity. Lange and co-workers (1993) suggested that mercury accumulation in bass is strongly influenced by chemical conditions of the lakes they studied. A strong relationship appears to exist between elevated mercury in Florida largemouth bass and low pH waters from swamp or peat drainage (Brim et al., 1994a). Our results may be contrasted with freshwater lakes because saltwater is generally alkaline due to calcium carbonate buffering, and may not be as favorable for the uptake of methyl mercury. Additionally, *C. nebulosus* is found in areas such as Tarpon Bay where salinity fluctuates widely. Rates of uptake may vary between individual *C. nebulosus* depending on how long they use particular water bodies, and how chemical parameters fluctuate in these waters relative to conditions favorable for uptake. These rates may mask the influence of specimen weight on mercury concentration.

While we found a significantly lower ($p<0.001$) mercury concentration in *C. nebulosus* collected in 1998 than in 1990, it should be noted that all specimens we collected were above the level of 0.1 ppm that Eisler (1987) believed to be harmful to fish-eating birds. Therefore, it is possible that the federally endangered wood stork, *Mycteria americana,* and roseate tern, *Sterna dougallii,* in addition to many other fish-eating avifauna that use the refuge at various times of the year, may be exposed to levels of mercury capable of impairing physiological activity.

In Florida, major sources of atmospheric mercury have been found to be municipal solid waste combustors (MSW), the electric utility industry and medical waster incinerators (Atkeson, 1999a). Natural sources of mercury in the state include mangroves, which have been found to play an important role in the cycling of mercury in the Everglades (Eisler, 1987).

The elimination of point-source discharges of mercury has been successful in improving environmental quality, although elevated levels of mercury may persist in contaminated areas long after the sources have been discontinued (Eisler, 1987). Current estimates suggest that ten years may pass before changes in mercury levels are detected (Atkeson, 1999b). Our results support a developing theory that mercury contamination levels, at least in certain areas of Florida, may be declining. The 1993 Florida Solid Waste Management Act required elimination of mercury from multiple commercial products and has reduced mercury content in municipal waste. Today it is estimated that there has been a 65% reduction in incineration of municipal solid waste in Florida (Atkeson, 1999b).

High concentrations of mercury in fish from remote areas suggests the complexity of natural mercury cycles and the human impact on these cycles (Brim et al., 1994a). A reduction in the concentration of mercury in the environment depends, in part, on the form of mercury, hydrodynamics, and physical and chemical conditions of the system (Brim et al., 1994a). A more detailed investigation into the natural and anthropogenic sources of mercury is needed to explain the changes that we found in levels of mercury contamination in *C. nebulosus* in estuarine waters of J.N. 'Ding' Darling National Wildlife Refuge. We recommend continued mercury analysis of *C. nebulosus* to gain a clearer understanding of any trends in mercury levels that may be occurring as represented by this species.

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OBSERVATIONS ON THE GROWTH OF WHITE VINE (*SARCOSTEMMA CLAUSUM*) IN A NUTRIENT-ENRICHED REGION OF THE NORTHERN FLORIDA EVERGLADES

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Abstract: The white vine (*Sarcostemma clausum*), historically a minor component of Everglades macrophyte communities, has undergone extensive population growth in a nutrient-enriched region of Water Conservation Area 2A in the northern Florida Everglades. Much of the herbaceous underlying vegetation (primarily cattail) has been severely impacted or replaced by accumulation of the vine. Here we present initial data on approximate aerial coverage, shoot growth, standing biomass, tissue nutrient concentrations, and experimental responses to soil nutrients and water depth. The ecological significance of *S. clausum* proliferation and potential implications for Everglades restoration and management are discussed.

Proliferation of invasive plants at the expense of native vegetation is an increasing problem throughout the world (Wade, 1997). Invasions frequently occur in response to environmental disruptions such as ecosystem fragmentation, alterations in resource availability, and/or physical disturbance (White and Pickett, 1985; Ewel, 1986; Hobbs 1989, 1991; Hobbs and Huenneke, 1992). Rapid population growth of opportunistic plant species under such conditions may lead to a partial or total loss of ecological structure and function of the native community (Holling et al., 1994).

Historically, the Everglades was composed of a number of distinct macrophyte community types as defined by associations of various indicator species (Loveless, 1959; Gunderson, 1994). However, large areas of this wetland are now dominated by plants that have either been absent from (exotic), or ecologically restricted within (native), these communities (Gunderson, 1994; White, 1994). Some of these vegetative changes have occurred in response to environmental change in the form of anthropogenic nutrient enrichment and altered hydrology (Davis, 1994; Light and Dineen, 1994). For example, where agricultural runoff and soil oxidation has resulted in elevated soil phosphorus (P) concentrations, sawgrass and open-water slough habitats have been replaced with monospecific stands of cattail (*Typha domingensis, Pers.)* (Jensen et al., 1995).

During May to July of 1998, a mixed community of willow (*Salix caroliniana, Michx.*) and cattail (*Typha domingensis*) in northwestern Water Conservation Area 2A (WCA-2A) of the Everglades became heavily over-

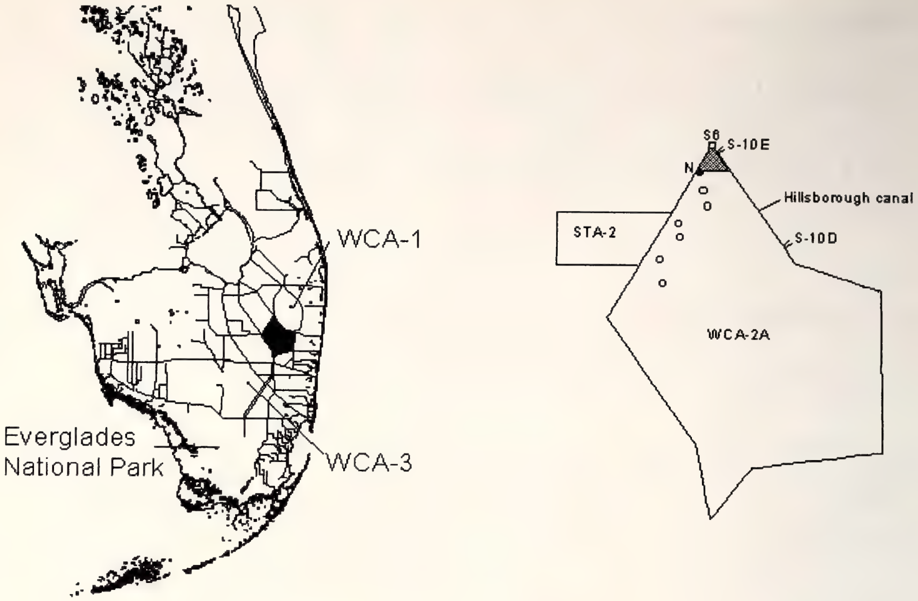

FIG. 1. Map of south Florida and the Everglades with approximate area of *S. clausum* coverage (shaded region within enlarged area) (WCA = Water Conservation Area, N = previously established monitoring station; open circles = new *S. clausum* sightings; S-10E = canal inflow structure; S6 = water control structure).

grown with the milkweed vine *Sarcostemma clausum* (Jacq.) Roemer & Shultes (Asclepiadaceae) (also known as "white vine"). Within this community, *S. clausum* has since grown to the point where it has become the dominant plant species and is associated with a significant decline in preexisting plants (Figure 1).

The status of *S. clausum* as a native or exotic species apparently remains in question (Jones and Jones, 1991). *S. clausum* likely expanded north from South and Central America, eventually becoming established in Texas, Florida, and the Caribbean islands. Most species of the genus *Sarcostemma* are associated with xerophytic communities (Holm, 1950; Allaby, 1992) and *S. clausum* is commonly observed in dry environments such as wooded slopes, sandy strands, savannas, and citrus groves (Holm, 1950; Bell and Taylor, 1982; Tucker and Singh, 1993). However, *S. clausum* is also classified as an obligate (OBL) or facultative wetland (FACW) plant according to the1996 National List of Vascular Plant Species that Occur in Wetlands (U.S. Fish and Wildlife Service) and can be found growing in the standing water of swamps, marshes, and canals (Godfrey and Wooten, 1981).

From the limited accounts that exist, it appears that *S. clausum* has been a relatively minor component of Everglades macrophyte communities over the last 50 years. Loveless (1959) observed *S. clausum* intermingled with other vines in tree islands in WCA-2A. Zahina and Richardson (1998) reported individuals scattered within cattail stands, willow-dominated tree islands, and on dry levees. Gunderson (1994) lists *S. clausum* as a species common to willow-heads while Zafke (1983) and Davis (1994) recorded its occasional presence in sawgrass communities of WCA-3A. In Everglades National Park, Busch and co-workers (1998) cited *S. clausum* as an infrequent inhabitant of wet prairie communities. Recently, however, Vaithiyanathan and Richardson (1999) have reported the proliferation of this species in the northeastern part of WCA-2A, an area that has been heavily impacted by nutrient-enrichment. This information suggests that under certain conditions, *S. clausum* has the ability to spread very rapidly.

In this paper, we describe a region in northwestern WCA-2A in which *S. clausum* has undergone extensive population growth. The area lies in close proximity to Stormwater Treatment Area 2 (STA-2), a constructed wetland designed to remove excess nutrients from agricultural runoff before being discharged into WCA-2A. The eventual delivery of this water into the marsh will affect the nutrient and hydrological character of areas some distance downstream and may consequently impact the existing flora and fauna, including *S. clausum.* The kind of invasive growth that has been observed thus far reveals its potential to become a significant pest under certain conditions. However, the scant literature that exists on this species is generally limited to aspects of biogeography, taxonomy, and associated insect species. Information on population growth and physiology appears to be totally lacking. In an effort to provide new data within this context, we measured shoot growth, standing biomass, and tissue nutrient concentrations of *S. clausum* in the field. We also documented growth responses to experimental manipulations of soil nutrients and water depth.

METHODS—*Study area*—We first noticed the presence of *S. clausum* in this area in May 1998. Approximately two months later (July) we observed that large areas of cattail had been covered and essentially replaced by the vine. We conducted a reconnaissance by helicopter in February 1999 which revealed the approximate area over which *S. clausum* had become a conspicuous component of the macrophyte vegetation (as determined by Trimble™ GPS) (shaded portion of WCA-2A in Figure 1). The zone encompassed an area of approximately 2.7 km^2 (~675 acres) in which the vine had achieved 100% cover in many places. This region of WCA-2A lies at a higher elevation than interior regions and currently receives water only through direct rainfall and limited discharge from the Hillsborough canal through the S-10E inflow structure (Figure 1). Consequently, this area of marsh experiences a comparatively shortened hydroperiod (Fitz and Sklar, 1999). The Hillsborough canal itself drains a 146 square mile portion of the Everglades Agricultural Area and soil TP concentrations near canal discharge structures greatly exceed interior marsh levels (DeBusk et al., 1994; Smith et al., 2000).

Within the vine-dominated area, two transects were established. We oriented the transects in directions of 200° and 180° (from magnetic North) extending from just south of the S6 water control structure into more interior regions, corresponding with the widening marsh boundaries from that point. Along each transect, 5 sampling sites were established approximately 0.3 km apart (total of 10 sampling locations).

Sampling—Shoot growth—At each sampling site, 5 individual vine stems were marked approximately 10–15 cm from the shoot apex with a short length of flagging tape. The length of each shoot from the tape marker to the shoot apex and number of leaves on each segment were recorded on a monthly basis. A crude measure of shoot growth rate (SGR) was calculated as increases in shoot length (cm) per day. Changes in the number of leaves per shoot segment per day (ΔLEAVES) were also calculated. Water depths were recorded with a meter stick.

Tissue nutrients and biomass—From three locations along each transect (n = 6) in February 1999, multiple live shoot segments (stem and leaves) were clipped and placed in coolers filled with ice for transport back to the laboratory. The tissues from each locations were dried at 60°C for one week and analyzed for total nitrogen (TN) and total phosphorus (TP) by standard methods (USEPA, 1983).

In July 1999, *S. clausum* was harvested from 0.25m^2 quadrats (n = 10) that were randomly placed within areas of vine at five of the ten transect locations. All above-ground biomass (live and dead) within the boundaries was clipped, dried at 60°C for 1 week and then weighed to determine dry weight/m^2 of vine biomass.

Responses to experimental manipulations of soil nutrients and hydrology—Segments of vine that included shoot apices (~ 25 cm long) were collected in the field and transported back to an outdoor botanical research facility. The segments were inserted into standard potting soil and within 10 days most had developed roots from the lower stems and exhibited some new growth. Twenty-eight of these plants were then individually potted in 15 cm diameter containers in either nutrient-enriched soil from the vine-dominated area or in unenriched soils from the interior of WCA-2A. One inch diameter PVC poles were inserted into the pots as a means of support for the vine. Previous analyses of soils from the enriched area showed TP concentrations in the top 10 cm to exceed 800 mg/kg whereas interior soils were less than 500 mg/kg (DeBusk et al, 1994; Smith, unpublished data).

Half of the plants in each soil type were immediately subjected to flooded (water level ~10 cm above soil surface) or wet (water level ~5 cm below soil surface) conditions created within two large (4m^2) fiberglass tubs. Plants in enriched soils were initially supplied with regular tap water while unenriched plants received reverse osmosis water. Accordingly, four different growing conditions were created (with 7 replicate plants per treatment), those being wet-enriched (WE), flooded-enriched (FE), wet-unenriched (WU), and flooded-unenriched (FU). Water levels were subsequently maintained by natural precipitation with excess water being allowed to drain out through holes in the sides of the containers. Shoot lengths and number of leaves were recorded before and after 1 month of growth in these conditions (May 18–June 18, 1999) and used to calculate percent increases in shoot length ((final-initial)/initial × 100; %SL) and percent change in number of leaves ((final-initial)/initial × 100; %LEAVES).

While %SL data exhibited normality and homogeneity of variances, log-transformations were used on %LEAVES to meet these criteria. The data were then subjected to two-way analysis of variance (ANOVA) with soil status and water depth treated as random factors. Individual treatment means were compared by Tukey's tests ($\alpha = 0.05$).

RESULTS—*Shoot growth*—The data presented in Figure 2a and b represent the first 8 months of monitoring from January to August, 1999. Mean SGR was lowest during the winter months of January to March and increased thereafter. Mean values (all stations combined) ranged from a minimum of 0 cm/d in February to a maximum of 3.96 cm/d in August (Figure 2a). The absolute maximum SGR value recorded was 6.68 cm/d in August. Cessation of growth of many shoots in February coincided with the production of flowers. The ΔLEAVES data exhibited a similar pattern to shoot growth with maximum mean and absolute values occurring in August (Figure 2b). Correlation between growth rates and water depths could not be

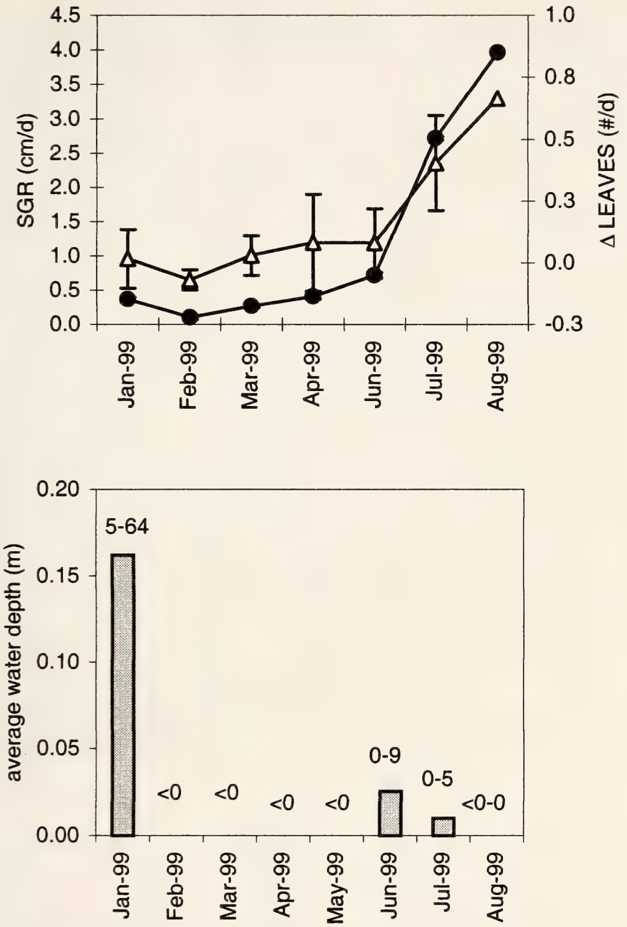

FIG. 2. Grand means of a) shoot growth rates (solid circles), change in number of leaves (open triangles), and b) mean water depths by date (water depth ranges in parentheses).

determined, primarily because standing water was absent for several months. However, growth rates increased during both marsh drydown (January to March) and reflooding (May to July).

Tissue nutrients and biomass—*S. clausum* shoots had mean TN and TP concentrations of 21,433 ± 2420 and 2,462 ± 410 mg/kg, respectively. TN ranged between 14,500 and 29,100 mg/kg while TP ranged between 1,200 and 3,740 mg/kg.

The mean dry weight of above-ground *S. clausum* biomass from the ten replicate samples harvested in July 1999 was 745 ± 136 g/m^2, ranging between 239 and 1654 g/m^2.

TABLE 1. Comparison of *S. clausum* above-ground biomass (AGBIO), leaf total nitrogen (TN) and leaf total phosphorus (TP) to *T. domingensis* and *C. jamaicense* from an enriched region of WCA-2A (TN values for *T. domingensis* and *C. jamaicense* are estimated from figures contained in referenced article).*

Macrophyte	AGBIO (g/m^2)	TP (mg/g)	TN (mg/g)
T. domingensis	690	1.2–3.2	~9.5
C. jamaicense	1,296	0.6–1.2	~11.0
S. clausum	745	1.2–3.6	14.5–29.1

* Miao and DeBusk (1999), Miao and Sklar (1998), this study.

Responses to experimental manipulations of soil nutrients and hydrology—For %SL and %LEAVES, soil and water depth effects were not significant although their interaction was (Table 2). In this regard, optimal conditions for the growth of the experimental plants were wet-enriched soil (Figure 3a). Mean %SL was significantly higher in wet-enriched compared to all other treatment groups. Flooded-enriched conditions yielded higher %SL values than wet-unenriched soils but were similar to flooded-unenriched treatments. In terms of %LEAVES, wet-enriched conditions yielded a large gain (Figure 3b). Leaf numbers in the flooded-enriched treatment also increased but %LEAVES was significantly lower than in the wet-enriched group. Plants in the two unenriched treatment groups lost leaves and their mean %LEAVES values were statistically lower than both the enriched groups, but similar to each other.

DISCUSSION—Shoot growth in *S. clausum* can be extremely rapid, as indicated by the maximum measured rate of nearly 7 cm/d. Growth rates showed large seasonal variability, which may be related to reproduction or other environmental factors such as temperature and irradiance. Although growth rates continued to rise as the marsh dried out during January to May 1999, these rates did not diminish with rising water levels from May to July 1999. Responses of the experimental plants to soil nutrient status and hydrology support this hypothesis. However a recent high water event from

TABLE 2. Table of statistical results from nutrients—hydrology experiment (ANOVA, random-effects model).

Measure	Effect	MS Effect	df Error	MS Error	F	P-level
% SL						
	Nutrients	237425	1	61403	3.86	0.29
	Water depth	15870	1	61403	0.25	0.70
	Interaction	61403	24	5983	10.26	0.003
% LEAVES						
	Nutrients	35.52	1	5.09	6.98	0.23
	Water depth	0.90	1	5.09	0.18	0.74
	Interaction	5.09	24	0.55	9.31	0.005

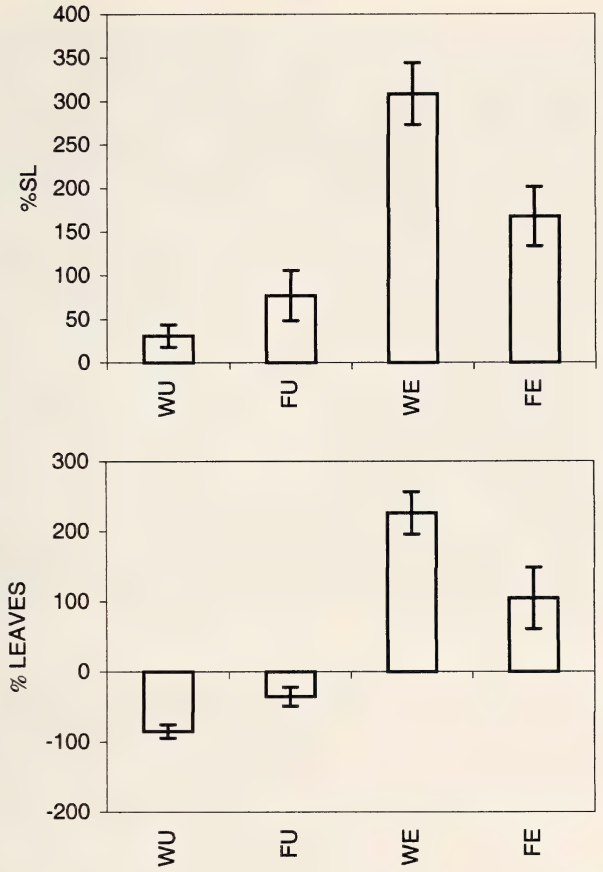

FIG. 3. Mean a) shoot length increases and b) change in number of leaves by nutrient-water depth treatment (WU = wet-unenriched, WE = wet-enriched, FU = flooded-unenriched, FE = flooded-enriched).

Hurricane Irene precipitation (October 1999) resulted in a considerable decline in the growth of *S. clausum.* Figure 4a reveals a virtual carpet of what appeared to be dead vine draped over an area formerly dominated by cattail, willow, and leather fern (*Acrostichum* spp.). However, we have since observed the emergence of new shoots from this material, an indication of senescence rather than mortality (Figure 4b). Clearly, more data is needed to elucidate the individual and interactive influence of hydrology and nutrients on the growth and survival of this species.

Biomass estimates indicate that *S. clausum* has produced more total above-ground plant material than what has been previously reported for cattail in enriched areas of northern WCA-2A (Miao and Sklar, 1998; Miao and DeBusk, 1999) (Table 1). Cattail invasion of the northern Everglades has been attributed to its capacity for high rates of nutrient uptake. However, nutrient levels within *S. clausum* tissues were even higher. In this regard,

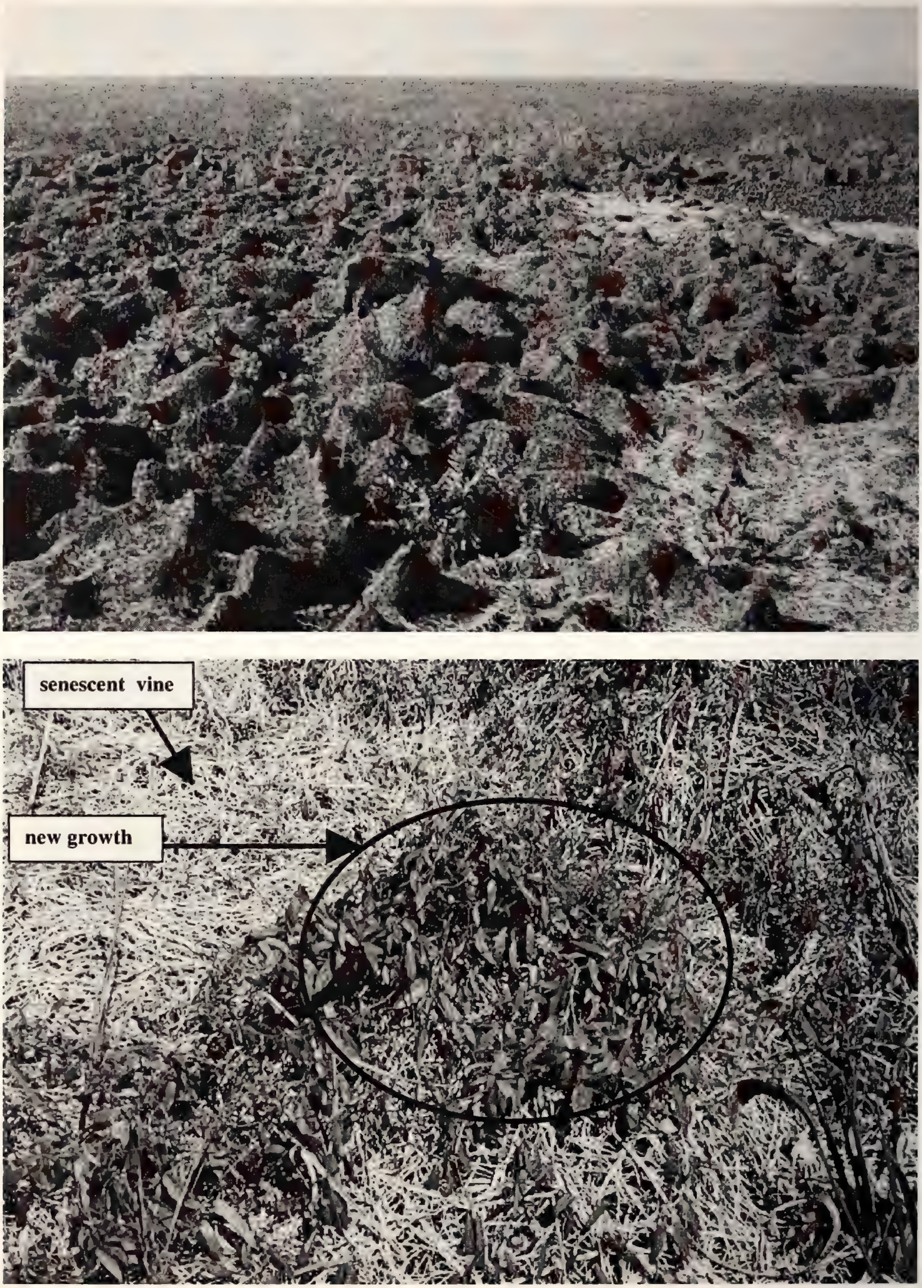

FIG. 4. Photographs of *S. clausum* a) coverage over landscape after Hurricane Irene high water event (November 1999) and b) subsequent regrowth from senescent vine stems (March 2000).

mean TP concentrations exceeded those found in cattail shoots from other nutrient-enriched areas of northeastern WCA-2A (Table 1) (Miao and Sklar, 1998; Miao and DeBusk, 1999 and references therein). TN concentrations were more than twice as high compared to cattail (Miao and Sklar, 1998).

Ecological significance—The most visually obvious effect of *S. clausum* population growth has been a significant decline in much of the underlying vegetation, presumably as a result of reduced light penetration and physical constrictions imposed by vine growth. Herbaceous plants such as cattail are particularly susceptible as they become bent over (and eventually broken) in the process of accumulating increasing amounts of vine biomass and some plants become physically restrained from growing in a standing position. This may eventually lead to root mortality if water depths rise to exceed the height of emergent leaves (Jordan and Whigham, 1988). Sawgrass may be somewhat more resistant due to its rigid structure as are the various shrubs and trees. However, we have observed small willow saplings that have been pulled to the ground and killed solely by vine growth.

A significant increase in *S. clausum* abundance may affect some aspects of food web ecology. For example, *S. clausum* is known to attract (as food plants) the butterflies *Danaus plexippus* (Monarch), *Danaus gilippus* (Queen), and *Danaus eresimus* (Soldier) (Minno, 1997). In the field, we have also observed large numbers of the Oleander aphid *Aphis nerii* (Rothchild et al., 1969) and milkweed bugs (*Oncopeltus fascatus*) (Milne and Milne, 1980) on actively growing shoot tips of *S. clausum.* Other interactions on milkweed plants in general include ladybird beetles, ants, lizards, birds, various soil organisms, and predatory mites.

Our experimental data suggest that although *S. clausum* may be very tolerant to flooding, its growth is reduced under such conditions. In deeper water its competitive ability in relation to other marsh plants (e.g., cattail) may be insufficient to maintain dominance within the macrophyte community. Field observations are somewhat contradictory, however, as no symptoms of significant deterioration appeared when the marsh was constantly flooded from October 1998 to January 1999. Moreover, portions of lower stems that are inundated quickly grow adventitious roots and may be able to assimilate nutrients directly from the water column. In this way, the benefits of increased nutrient supply from canal discharge may ameliorate or surpass any negative effects of higher water levels.

Although the total area over which *S. clausum* has become a dominant species is relatively small compared to WCA-2A as a whole, its potential to spread may be high. Many invasive plants demonstrate a lag phase before population explosions (Hengeveld, 1989) and it has been hypothesized that certain species build up cumulative populations of individuals or seed banks that can help trigger such events (Hobbs, 1989). The seeds of *S. clausum* are wind-dispersed, allowing them to reach areas some distance away from existing populations, unlike many other marsh species with water-borne seeds. The expansion of *T. domingensis* in the northern Everglades, and of invasive plants in general, has been linked to this reproductive characteristic (Miao and DeBusk, 1999; Wade, 1997). *S. clausum* is also capable of flowering multiple times per year (Holm, 1950) and any further augmentation of the seed bank would presumably increase the potential for *S. clausum* to proliferate in this way, in addition to vegetative reproduction from rhizomes.

We have observed *S. clausum* at several other locations in WCA-2A where it has previously been absent. These locations (indicated by open circles in Figure 1) represent permanent sampling platforms (established as part of a separate study) that were constructed in October 1997. The sites lie directly downstream from STA-2 outflow and will experience hydrological and nutrient regimes associated with STA discharge. Discharge of STA water with TP levels higher than ambient concentrations may potentially stimulate the growth of existing *S. clausum* plants and/or the germination of seeds. Accordingly, further studies are needed to assess the potential for this species to have a significant impact on macrophyte communities in this region and throughout the Everglades. Regardless, the current proliferation of *S. clausum* is further evidence that Everglades macrophyte communities may, under certain environmental conditions, be very dynamic.

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ERRATUM

Meshaka, W. E., Jr., W. F. Loftus, and T. Steiner. 2000. The herpetofauna of Everglades National Park. Florida Scient. 63(2):84–103.

In Table 1 values for *Diadophis punctatus punctatus* and *Drymarchon corais couperi* should each move one column to the right. Habitat for *Gopherus polyphemus* should be Dune instead of Estuarine, and for *Kinosternon baurii* habitat should be estuarine not marine. Sums for Dune should read 2 and Marine should read 7. *Pseudemys floridana peninsularis* should replace *Pseudemys floridana floridana.* Line 32 on p. 97 should read“Among the rat snakes, two recognized forms. . .” instead of “Among the rat snakes, the two recognized forms. . .”

W. E. M., Jr.

REVIEW

Roger A. Morse, *Richard Archbold and the Archbold Biological Station,* University Press of Florida, Gainesville FL. Pp.104 (6 X 9). Price $29.95.

ARCHBOLD Biological Station, a 5000-acre estate located near Lake Placid, Florida is world famous because of a unique ecosystem, the Florida Scrub, and because of the many outstanding scientists who were attracted to do research there. Their work has often appeared in the pages of the *Florida Scientist* and many other refereed journals. What is less well known is who was Archbold and how the Station came to be. In this volume, the author, a retired professor of apiculture at Cornell University, provides the answers in an interesting, readable account. Richard Archbold (1907–1976) was the grandson of John D. Archbold, second president of Standard Oil. The grandson, Richard, though not a college graduate, became a well-trained biologist through personal experience and exposure to others, first as an attachment to an expedition to remote jungles of Madagascar (1929–1931). Though the expedition was under the auspices of the American Museum of Natural History, it was largely financed by Richard Archbold's father. It was a sound investment in science and a 22-year old son, who would later be the moving force behind three expeditions to the jungles of New Guinea in the 1930s and later to the unique ecosystem near Lake Placid. Richard Archbold was a quiet man, who attracted the favorable attention of many, including Lowell Thomas. To paraphrase Dean Amadon, Archbold was a man who yearned to be an explorer, a biologist, and he had the resources—financial and intellectual—to fulfill his ambitions and to make it possible for others to follow. The book is a tribute to a dedicated philanthropist, but it also tells the interesting story of those who followed and benefitted from the example and endowment of Richard Archbold.—Dean F. Martin, University of South Florida, Tampa.

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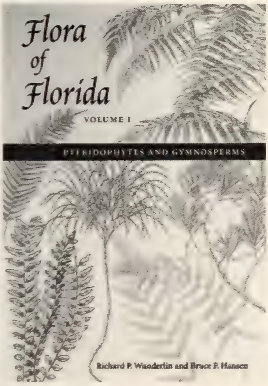
Bottlenose Dolphin
BIOLOGY AND CONSERVATION
John E. Reynolds III, Randall S. Wells, and Samantha D. Eide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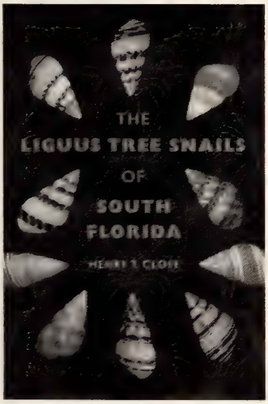

The Bottlenose Dolphin

Biology and Conservation

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CONTENTS OF *FLORIDA SCIENTIST* VOLUME 63

Number One

An Experimental Test of the Predator Satiation Hypothesis: At What Level Might It Apply? .... Stephanie S. Romañach and Douglas J. Levey 1
Analysis of Commercial Selenium-Supplement Tablets .... Kathleen M. Carvalho, Robert F. Benson, Francis A. Booth, M. Jordan Collier, and Dean F. Martin 8
Florida's Wax Palm: The Silver Form of *Serenoa repens* (Arecaceae) ...... Frederick B. Essig, Y. Renea Taylor, and Diane TeStrake 13
Wildlife Use of a Created Wetland in Central Florida .... Donald M. Kent and Michael A. Langston 17
Influence of Distance and Post-Fire Recovery on Accuracy of Hand-Held Radiotelemetry in Forested Landscapes in Southwest Florida .... Martin B. Main, Ellen Cheng, Betty Harper, and Larry W. Richardson 20
Inventory of Fishes of Everglades National Park .... William F. Loftus 27
The Influence of Seawalls and Revetments on the Presence of Seagrass in the Indian River Lagoon, A Preliminary Study .... Steve Nielsen, Bill Eggers, and Sharon Collins 48
Book Review .... Frederick B. Essig 62
Books Received 63

Number Two

Ages of Two Speleothems from Florida Caverns by U-Series Dating Methods .... J. K. Osmond and Adel A. Dabous 65
Evaporation and the Precipitation-Evaporation Balance in Florida Bay ...... Ned P. Smith 72
The Herpetofauna of Everglades National Park .... Walter E. Meshaka, Jr., William F. Loftus, and Todd Steiner 84
A New Record for *Schistocerca ceratiola* (Orthoptera: Acrididae) .... Jason M. Squitier 104
A Comparison of Scrub Herpetofauna on Two Central Florida Sand Ridges .... Lyn C. Branch and D. Grant Hokit 108
Use of a Computer-Interfaced System for Determination of the Inhibition of Oxygen Production by Selected Aquatic Weeds in the Presence of Cattail (*Typha domingensis*) Extracts .... Dawn M. Ambrogio, Maria T. Gallardo, Robert F. Benson, and Dean F. Martin 118

Isotope Analysis of Galena from Prehistoric Archaeological Sites in South Florida ....
Robert J. Austin, Ronald M. Farquhar, and Karen J. Walker 123

Number Three

Remediation of Selenium Contamination by Plants and Microbes: An Annotated Bibliography ....
Kathleen M. Carvalho, Maria T. Gallardo, Melissa J. McGettigan, and Dean F. Martin 133

Temporal Dynamics of Zooplankton Community Composition and Mean Size at Lake Wauberg, Florida ....
Kimberly I. Tugend and Micheal S. Allen 142

An Experimental Analysis of Maze Learning in the Wolf Spider, *Trochosa parthenus* (Araneae: Lycosidae) ....
Fred Punzo 155

Mycorrhizal and Nitrogen-Fixer Associations with *Casuarina* spp. and Mycorrhizal Associations with *Melaleuca quinquenervia* in Everglades National Park ....
Andre J. Cantelmo, Sylvan R. Kaufman, and Jeanmarie Hartman 160

An Approach on Improving the Health of Human Populations ....
Jay W. Palmer 167

Sexual Dimorphism in Vestigial Pelvic Bones of Florida Manatees (*Trichechus manatus latirostris*) ....
Derek M. Fagone, Sentiel A. Rommel, and Meghan E. Bolen 177

Late Pleistocene (Rancholabrean) Records of the Harvest Mouse (*Reithrodontomys*) in Florida ....
Dennis R. Ruez, Jr. 182

Outstanding Student Paper Awards ....
Ernest Estevez 191

Number Four

Biogeography of Amphibians and Reptiles of the Sea Islands of Georgia ....
Joshua Laerm, Nikole L. Castleberry, M. Alex Menzel, Robert A. Moulis, Gerald K. Williamson, John B. Jensen, Brad Winn, and Michael J. Harris 193

Prey Selection by a Maternity Colony of Big Brown Bats (*Eptesicus fuscus*) in the Southeastern United States ....
Michael A. Menzel, Timothy C. Carter, Brent L. Mitchell, Loren R. Jablonowski, Brian R. Chapman, and Joshua Laerm 232

Biology and Ecology of *Rivulus marmoratus*: New Insights and a Review .... D. Scott Taylor 242
An Evaluation of Mercury Levels in Spotted Seatrout, *Cynoscion nebulosus*, in Tarpon Bay, J.N. "Ding" Darling Wildlife Refuge, Sanibel, Florida, with Reference to Previous Studies .... James V. Locascio and Paul J. Rudershausen 256
Observations on the Growth of White Vine (*Sarcostemma clausum*) in a Nutrient-Enriched Region of the Northern Florida Everglades .... Stephen M. Smith, Patrick B. Garrett, Jennifer A. Leeds, Julie Brewer, and Paul V. McCormick 261
Acknowledgment of Reviewers 273
Erratum 273
Book Review 274

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